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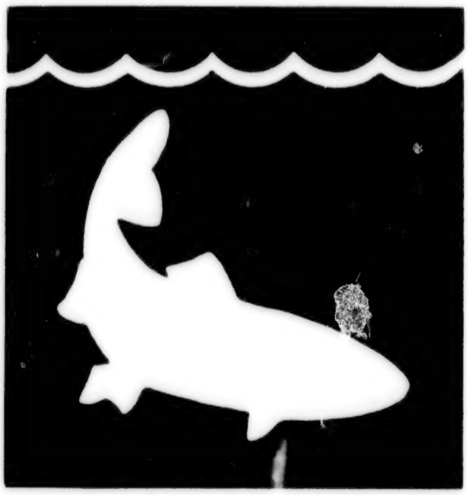
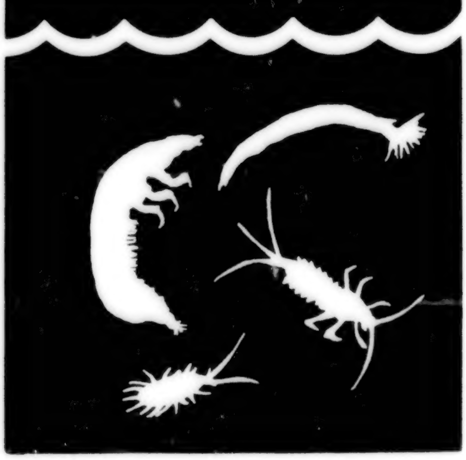


INVERTEBRATE FISH FOOD RESOURCES OF LOTIC ENVIRONMENTS

INSTREAM FLOW INFORMATION PAPER: NO. 24

BIOLOGICAL REPORT 88(13)
JUNE 1988



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Biological Report 88(13)
June 1988

INVERTEBRATE FISH FOOD RESOURCES OF LOTIC ENVIRONMENTS

Instream Flow Information Paper No. 24

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PREFACE

As we learn more about and have to deal with more aspects of man's environment a paradox develops. On one hand, the increasing size of the knowledge base in a subject area encourages the development of parochialism in the professions. On the other hand, the resource management concerns have been expanding in number and professional complexity. As more concerns enter the resource management arena, managers know proportionally less about each of the specialties involved. Technology is relatively boundless compared to the limitations of human time and capability.

This volume integrates some of the knowledge of benthology with some of that of fisheries. The benthos feed the fish, and the fish stress the benthos. Twenty or thirty and more years ago these subjects were one and the same in scientific journals and academic curricula. Today, a biologist interested in both the fish and their food would need to participate, at a minimum, in both the American Fisheries Society and the North American Benthological Society to keep abreast of the knowledge being developed. To further complicate the issue, the greatest impact on either resource is the product or by-products of man's endeavors that affect the aquatic resources he wants to use.

For a few years this volume should suffice as an aid to comprehension of fish and their food problems. It will need future revision and integration of new knowledge. Because of time and capability limitations the scope was restricted to flowing water habitats. If the aquatic specialists interested in rivers communicate, a working consensus can be reached for the management of the resource. With good management the resources can persist and be productive for man. Riverine life's primary problem is the elimination of its base of habitation as we divert and consume the water or impound it to create storage lakes for other uses. Riverine habitat is not simply in a conflict of uses in management, it is being rapidly usurped out of existence. No one is building rivers to replace those lost through alteration and misuse. Efforts to maintain existing river habitat or to restore damaged habitat are minuscule.

SUMMARY

Fish are the aquatic ecosystem's end product harvested by man. Food supply may regulate the production of fish. This report deals with analysis and evaluation of fish food stocks. The scope is limited to river habitats and their invertebrate supplies of food. Information is most applicable to smaller streams or rivers--up to mean annual discharges of approximately 1,000 cfs. Streams of this size cover approximately 99%, based on river miles, or 50%, based on surface area, of the Nation's total. In larger rivers (e.g., Mississippi, Columbia), the ecosystem becomes more complex, and information bases and technology are limited; the information provided here is less applicable to such rivers because of our limited understanding.

Most fish populations are not restricted by food resources. If the fish are in good condition and growing at an acceptable rate (determined by examining the fish), we can assume that their fish food supply is adequate. If problems are encountered in the fish stocks, food may be but one of the factors. This document also discusses aspects of analyzing fish stocks.

Changes in river morphology or water regimen, for example, are recognized factors affecting fisheries potential. Any planned waterway alteration raises questions as to the impacts on fisheries resulting from say, habitat or water quality changes anticipated. The Instream Flow Incremental Methodology attempts to systematically evaluate the changes in fish habitat to minimize impacts of planned changes. Fish "space" must also consider the quantity and quality of space available for fish food production.

Natural resources agencies have dollar and manpower limitations. If the fish stocks appear to be food limited, this document discusses the current technology to evalute the supplies. If changes will be effected in a river, we must maintain certain conditions to ensure that food production will be adequate to sustain the fish in their new habitat. The physical conditions required to sustain or enhance the food supply are discussed.

Analysis of fish stocks to determine growth rates and condition factors should be a manager's first effort. If species are growing at adequate rates, food is not a factor. Low numbers of fish usually are not a food related problem. Stunted and skinny fish may occur even with good food production and may reflect problems within the fish community, such as an overabundance of a species, parasites, etc. In such cases, the paramount problem is the fish stocks and their management. Until there is a reasonable assurance that food shortages are a likely problem, food investigations may be more subjective exercises than objectives to a goal of enhancing a fishery. Evaluation of fish food stocks are specialized efforts that consume money and time. Planning a useful food study should be based on reasonable need and adequate resources.

Emphasis is placed on the macroinvertebrate (visible to the naked eye) food animals. These are the primary food items of the carnivorous sport and food fishes (e.g., trout, bass, etc.) that are of high management interest.

Habitat available within a stream dictates both the kinds of food animals that will predominate in the supply and the potential total supply. Individual food species require specific habitats. Fish as opportunistic feeders are more affected by the total food supply than by the supply of specific food animals. Diversity of species has a lesser impact, but remains important in stream fisheries management. Diverse species life-cycles provide a seasonal continuity of food supply because availability of many species is seasonal.

Measurement of the quantity of fish food is complicated if not impossible under many situations. Measuring standing crop can be achieved quite readily; however, these data have limited meaning relative to the food produced. If the standing crop were the annual production of food the quantity of fish flesh produced would be very small. In streams, there are several "crops" of food produced. The problem is determining the total mass produced in a growing season.

The production potential of benthic organisms produces populations that exceed habitat carrying capacity. Competition for the stream's bottom habitat forces surplus animals to migrate. This results in a portion of the animals being in temporary suspension (drift) in the water column. The drift animals are the primary food supply of many fish. Being surplus, their consumption has no effect on the continued success of the food species. Stream fish occupy space of little importance to the production of their food. Most stream fishes are rarely found "grazing" in the best food production areas, rather, the currents deliver food to the fish's habitat.

Typically, the quantity of drift reflects the production of benthos. Streams with average production rates have approximately 1.5% to 2.0% per day increase in benthos. This percentage of the benthic standing crop can be measured as drift animals in the water column. This equates to an annual drift biomass of five to seven times the measured standing crop. The drift animals are the net food production available to the fish. With five to seven times the standing crop equalling the total annual fish food resources, a typical stream would produce 700-1,000 kilograms of fish food per hectare. Assuming a 10% conversion efficiency to fish biomass, this food supply should support fish production of 70-100 kilograms per hectare per year (28-40 pounds per acre). This is the typical range for wild fish production.

Periodic sampling of benthos standing crop and drift could give the manager more useful information than has been available in the past. Basic knowledge that one stream is more productive of fish food than another (e.g., daily drift rates of 0.5% versus 3.0% of the standing crop) would be useful in many fish management programs. Periodic sampling throughout the year is not prohibitive. Actually, the basic information is available with the sampling of both benthos and drift, to calculate total fish food produced. If a stream's fish yield is not proportional to its fish food production, other management options may be necessary. If food appears to be limiting fish production, then emphasis on enhancing fish food production may be the appropriate step for the manager to take.

Several species of fish food organisms in streams require certain velocities and depths. Data available on these rheophilic (current loving) species indicate the following physical habitat characteristics are optimum:

Velocity	1.8 to 2.0 feet per second
Depth	4.3 to 7.5 inches
Substrate size	mixed small to medium cobble

A habitat with these characteristics, however, is not the most productive of fish food biomass. These species provide a continuum in food availability, which might not occur if their habitat were not present. Other food species habitat will occur along stream banks and in river pools.

Aquatic vegetation, logs, or debris in a stream increase the physical habitat available for benthic animals. A method is presented to estimate the area of habitat available from tree remains in a stream.

A "key" is presented to aid managers in a cursory examination of fish and fish food information. The key assists in narrowing the range of potential problems managers need to consider in evaluating a river's biological resources.

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ACKNOWLEDGMENTS

In the mid-1970's, several Federal agencies recognized that a major problem in managing river resources was excessive dewatering due to diversion and consumptive use. To address the problem of how much water had to be retained in a stream to maintain its biological uses, the agencies united to develop a cadre of expertise under the aegis of the U.S. Fish and Wildlife Service. The Cooperative Instream Flow Group (IFG) within the Service's National Ecology Research Center in Fort Collins, Colorado, was to determine the instream flow needs that must be maintained to perpetuate the ecologic and human uses of rivers. A core of Fish and Wildlife cadre was supported through interagency assignment of funds or personnel to the group. In 1981, I had the good fortune of being assigned to IFG for two and one-half years by my employer, the U.S. Environmental Protection Agency (EPA).

Among the many users of a river are its fishes. One of the primary efforts of IFG was to determine the optimum and minimum quantities of water needed in a river to maintain the fishes. "What about food to sustain the fish?" was a question that had not been addressed. After learning that I had over a decade of experience with productivity and benthos, Clair Stalnaker, IFG Leader, requested that I undertake a critical review of the fish food resources of rivers. This volume is that review.

The draft was 80% completed when I returned to EPA, where Patrick Tobin, Water Criteria and Standards Division Director, encouraged periodic diversion to complete the manuscript and revise it through its drafts.

In 1985, draft copies were distributed for comment and critique to several colleagues. Sincere thanks and acknowledgment of the reviews received are extended to:

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INTRODUCTION

The purpose of this volume is to guide the investigator in evaluating food resources for stream fish. The fish food in lakes will not be discussed except when occasional excursions are necessary as examples. The reader should remember though that some large rivers approach lakes in their limnological characteristics. The navigation pools of the Ohio and upper Mississippi Rivers are more lake-like than they are akin to the Au Sable Rivers in either Michigan or New York. Many of the Nation's large rivers are now a series of man-made lakes, and the flora and fauna are more lentic than lotic in character and composition.

Riverine fish have the basic needs of any life form: food, shelter, and water. These needs must be met for all life-cycle stages, including eggs, sperm, and incubating embryos. The natural stream environment contains adequate water for the fish species native to it. Nowhere do we find fish per unit of water at populations as dense as can be sustained in an aquarium, fish farm, or fish hatchery, where water quality is manipulated, food is provided, and the animals are sheltered from enemies. Eggs of hatchery trout will incubate and hatch if kept moist with only enough water movement to transport a fresh oxygen supply to the respiring embryo and to carry away toxic metabolites generated by the embryo.

If a species is to flourish it must have a place for the adults to reproduce, a place for the eggs to incubate, and a place for each life stage. Habitat requirements vary from species to species. Incubating eggs may be attached to grasses, buried in coarse gravel, suspended in the water column, spread over the bottom, or deposited in nests that are sometimes guarded by the adults. Newly hatched sac-fry are planktonic, incapable of controlling where they are, and moved by the water as are their neighbors the algae, zooplankton, and bacteria. After consuming the maternal lunch given them in their yolk sac, they must begin feeding for the energy and nutrients required for maintenance of physiological processes and growth. With yolk sac absorbed, the fry becomes more streamlined and starts to swim in pursuit of food. Fry may graze on neighboring algal cells or prey on microscopic animals. This fish fry is a larvae, nearly as different from the adult of the species as a maggot is from the fly. With growth, its musculature will change, scales will develop, and teeth will form as it passes through the fingerling stage in its first year of life, which is followed by a year or more as a juvenile before it becomes an adult and reproduction of the species is possible. A fish's requirements for food, shelter, and water can change as the fish grows.

Food is a prime consideration when man is considering the well-being or management of fish stocks. How many fish? What kinds of fish? How fast do they grow? How big do they get? These are the concerns when we look at fish stocks as food or recreational resources. A stream occupied by small, skinny, slow-growing fish must be "poor range" or "short of food," at first thought of the manager. This may or may not be the case. The simplest way to find out if food is affecting the well-being of the fish is to evaluate the food resources, both availability and reliability.

The chemical and physical constituents of water must be within the tolerable range for the desired organisms. Water quality management is basically maintaining these constituents between prescribed limits. For many constituents these limits or criteria are known (EPA 1976). Man in his ingenious commerce, industry, and social aggregations, however, can produce new and usually unknown by-products that reach watercourses. The community of life will respond to these by-products, and the biologist can observe the effects before the physicists or chemists can detect or measure the adverse constituents. The concentrations of many water constituents must be maintained between minimum and maximum values; below or above there may be adverse effects on the resources.

The quantity of water in a stream varies naturally. Small streams may seasonally dry up for periods of time. Spring rains and melting snow may produce flood flows. The aquatic organisms of a waterway are adapted through eons of evolution to cope with such variances. Man in his endeavors requires the alteration of flow regimens and the diversion of water to useful places. The impact of these changes on the fishery resources is not well known. Water quantity managers have tried to guess at the impacts for several decades, with little or no technical basis as to water quantity effects on a stream's fishes. Within the past decade, a scientific approach to the water needs for the fishes has begun to be developed under the leadership of the U.S. Fish and Wildlife Service's Cooperative Instream Flow Group. Systems are now available to estimate the changes in stream usability by a species of fish when the water regimen is changed (Stalnaker and Arnette 1976; Bayha 1978; Bovee and Milhous 1978; Milhous et al. 1981; Bovee 1982).

In this report, I will discuss the evaluation of fish food resources and the environmental factors that affect the quality and quantity of food available to the fish stocks. The user will find that there is much to be discovered in this field. We may know more about the life histories of some of the food organisms than just whether a fish will or can eat them. For example, the freshwater drum (Aplodinotus grunniens) is known to incorporate quantities of mollusks in its diet (Scott and Crossman 1973) and is equipped with pharyngeal teeth, which are massive molars for crushing shells. These fish also consume other benthic animals in their bottom grazing habits and, if the opportunity appears, they will capture forage fish. It has long been assumed that small drum dieted on small benthos or planktonic animals until they had grown enough to cope with snails and clams. Recent investigations, however, revealed that the smallest larval drum are predators on other small fish (Clark and Pearson 1978). At an early larval stage, they have abnormally large mouths equipped with minute teeth for grasping and handling their prey. This period of development persists for several days only, and with further growth, mouth size diminishes in relation to the size of the fish, the teeth diminish to remnants, and the larvae continue their development feeding on microinvertebrates.

The investigation of fish food resources of a stream requires some field effort. The presence or absence of sufficient food resources can not be determined theoretically, calculated, or surmised from the laboratory or office.

The "Are the fish getting enough food?" question might best be answered by a study of the fish. If the fish growth rates and condition factors are normal when compared to neighboring streams or compilations of data (e.g., Carlander 1969, 1973), it can be assumed that they are getting a normal complement of food. By directly evaluating the well-being of the fish species, we also reduce or eliminate the problems of interpreting or extrapolating the food resources through a hypothetical food-web into the fish consumer. Theoretically, a simple food chain consists of 1 lb of fish built from 10 lb of mayflies fed by 100 lb of plant material. In reality, there are many fish food options derived from a variety and multiplicity of food sources. Fish have preferences for food items, but fish will not unduly exert themselves to search out select foods. The pursuit and capture of a 2-g insect-fed minnow may not be as efficient in energy and nutrient transfer as the consumption of 100 midge larvae weighing 2 g, but it is much more efficient for the individual consumer than exerting the effort for 100 individual pursuits. Animals are energy conservative and will not wastefully use energy unless there is a need for it; easy feeding is economical for the individual and for the species. Ambushing prey rather than active hunting is the general rule of the predator. Many stream inhabitants rely on the current to transport forage to their living spaces.

If the fish are slow-growing, slow-maturing, or skinny specimens, a shortage of food may be the problem. There are other environmental factors, such as inter- and intraspecific competition, water quality, shelter, temperature, that may be the cause of marginal habitat for the species. Food cannot be blamed as the problem until it is demonstrated to be the problem.

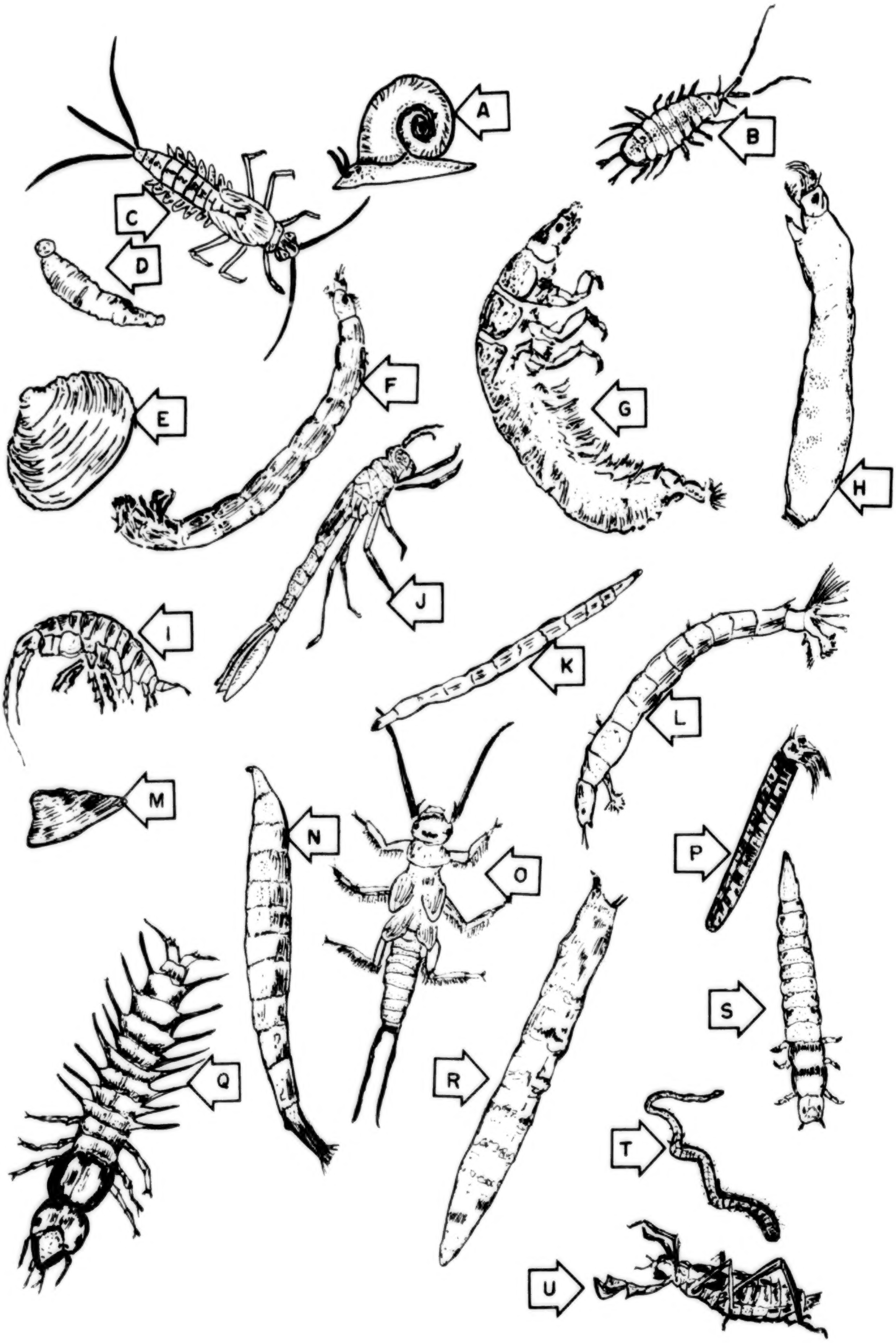
Streams change as they progress from headwaters to downstream reaches, and different reaches have characteristics that favor different species. The requirements for brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) are different, and the habitat may favor one species over the other, but not to the total exclusion of the less favored. Thus, one species may be in a state of well-being while the other is in poor condition. The brook trout could be prey for the larger brown trout, which then have the more efficiently gathered food supply compared to the insect larvae pursued by the brook trout. The stream manager must also be aware of which species are in optimal and which species are in suboptimal habitat. This determines which fish species is the easier to manage or produce in the stream reach. The prudent and practical manager must also be aware of what the fish-consuming public wants. It would be politically naive to manage a good catfish (Ictalurus spp.) stream for optimum catfish production when the fishing populace does not want catfish. A less optimum production of largemouth bass (Micropterus salmoides) and bluegills (Lepomis macrochirus) is offset by the public's desire for them and by the public's unwillingness to learn to fish for or use the catfish. The ecological system's most efficient use may not be the human's most efficient use, because humans can be lazy, resistant to change, and reluctant to learn new ways, just as are other species. Many trout streams are marginal trout streams; ecologically, their optimum production is vested in suckers, chubs, and minnows, which are largely unseen and unknown to the trout fishermen.

The types of fish food organisms discussed here are principally the macroinvertebrate, bottom-dwelling animals, or benthos. These animals will be retained on a U.S. Standard Number 30 Sieve, or are essentially those visible to the unaided eye. They crawl on, burrow in, or attach themselves to the bottom or fixed structures in the waterway, such as logs, aquatic plants, and manmade structures. They may at times intentionally or inadvertently be in the water column and thus are temporarily transported by currents, during which time they are called "drift," but they must return to the bottom niches for their survival and basic existence. Means of locomotion are restricted. Extended rapid migrations do not occur or they have a sessile, attached mode of life, and these habits limit the reach of stream an individual will occupy during its life span. There is a wide variety of these organisms; some examples are illustrated in Figure 1. The number of species is in the thousands and many new species are discovered each year. Except in specialized work, specific taxonomic identification is not required for fish food evaluation. It would be adequate to recognize that there were four kinds of mayflies present in the stream and that one burrowed in the mud and three crawled over, on, and under large rocks.

The benthos has representatives of all the major "life styles." There are grazers, detritivores, carnivores, filter feeders, and parasites. There are animals that live in constructed cases attached to the substrate with suckers, burrowing worms and larvae, sprawlers, and crawlers. Some body forms are soft, some light to heavily scleritized, and others are encased in shells. Many of the insects have terrestrial adult life stages. There are larvae, nymphs (a naiad is an aquatic nymph), subimagoes, imagoes, and eggs. Regardless of the life style or morphology they are all potential fish food at some time and place for some species of fish.

Measurement of fish food is usually as number or mass present at the instant of sample taking. This is the standing crop and is expressed in quantity per areal unit, e.g., pounds per acre, milligrams per square meter, kilograms per hectare. Most historical data are a mixture of metric and English units, the most common being milligrams (or grams) per square foot, because these are practical units that are close to the size and capacity of the sampling and analytical tools. Occasionally, standing crop will be on a mass per volume base, such as grams per cubic meter of water; these units are used for plankton or drift organisms. A mass per mass expression of data is sometimes used for macroinvertebrates living in or on quantities of vegetation. Quantity per mile of stream data can be found, but cannot be used for comparing streams because of varying widths of streams.

Productivity is a rate per unit of time, such as pounds per acre per year. It should not be used as a substitute for standing crop. The fish standing crop present in a stream may be the product of a considerable period of growth and accumulation to the time of observation and thus may represent either a high or low production rate (short or long term). Turnover is a concept that incorporates the life span of the species into productivity. Short-lived organisms may have several generations per year, or a rapid turnover in the species' productivity and the standing crop. Even though small in



A. Snail (Gastropoda, Mollusca) ×2
B. Aquatic sowbug (Asellidae, Isopoda) ×2
C. Mayfly nymph (Baetidae, Ephemeroptera) ×4
D. Leech (Hirunidae, Annelida) ×1
E. Fingernail clam (Sphaeriidae, Mollusca) ×4
F. Bloodworm (Chironomidae, Diptera) ×5
G. Caddis larvae, net spinner (Hydropsychidae, Tricoptera) ×5
H. Black fly larvae (Simuliidae, Diptera) ×5
I. Scud (Gammaridae, Amphipoda) ×2
J. Damselfly nymph (Zygoptera, Odonata) ×2
K. No-seeum larvae (Ceratopogonidae, Diptera) ×5
L. Midge larvae (Chironomidae, Diptera) ×5
M. Limpet (Gastropoda, Mollusca) ×3
N. Snipe fly larvae (Rhagionidae, Diptera) ×3
O. Stonefly nymph (Pteronarcidae, Plecoptera) ×1
P. Caddis larvae, case builder (Brachycentridae, Tricoptera) ×2
Q. Hellgrammite (Corydalidae, Megaloptera) ×1
R. Horse fly larvae (Tabanidae, Diptera) ×2
S. Riffle beetle larvae (Elmidae, Coleoptera) ×2
T. Worms (Tubificidae, Annelida) ×2
U. Dragonfly nymph (Anisoptera, Odonata) ×1

Figure 1. Selected fish food animals (x = magnification).

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size, the total quantity grown per unit of time may exceed that of larger, long-lived organisms.

An adult invertebrate has the potential to reproduce several hundred fold or more of its species. If all the eggs produced grew to adults it would be a short time before streams were bank full of the species. From the time of deposition to maturity each clutch suffers tremendous mortality, however, only two adults (male and female) per clutch need to survive to propogate the species. If only a fraction more than two survive, the population of the species will increase; if a fraction less than two survive, the population will decline. The biomass production of the clutch will greatly exceed the biomass of the two adults. The hundreds of immature specimens that died grew to varying sizes, and the sum of their biomass is added to that of the adults for the gross productivity of the species. Some of the specimens died from diseases, congenital defects, and accidents; their biomass is returned towards the base of the food web. Only a small fraction of the biomass decomposes to the stream's elemental nutrient pool, which supports the plant-based primary production. Many of the dead, decomposing, and mechanically disintegrating carcasses are intercepted and used as food by multitudes of scavenging invertebrates and fish. Their food value is thus intercepted and recycled upward again in the food web. Many immature specimens are captured alive by predatory invertebrates and vertebrates, and their energy and nutritional value are moved directly along in the food web. Only a percentage of the total biomass produced (gross production) goes into our product of concern (fish), and this is the net production or yield available to the consuming fish.

Earlier in this section I used the approximation of 10 lb of food to produce 1 lb of fish, or 90% of the fish food is not converted to fish flesh. A portion of this unused food is for energy to maintain the fish, and metabolites are excreted as respiratory and urinary waste products. Another portion of the consumed organisms is not assimilated from the digestive tract and passes back into the ecosystem as fecal material. Some fecal material decomposes to a chemical nutrient state, but much of it stays as particulate or pellet material to be consumed by invertebrates that can use it, thus again directing the nutrient and food value back along the food web. Very little of the biomass escapes the biological portion of the ecosystem. Even chemical metabolites, such as sugars and amino acids, tend to be absorbed and incorporated as life building-blocks. The ecosystem is very conservative in keeping food (energy and nutrients) in the biological state.

Mountain spring water contains no life in the aquifer; once exposed on the surface, plant life begins the building of biologicals. Terrestrial biological materials are swept by wind, rain, and runoff into the new water-course, and the animal life starts to use and conserve the materials. Detritus, organisms, and fecal materials are continually being intercepted, processed, and cycled by many species. As the stream progresses, more biological products and byproducts become available, and species capable of using them are found in the system. The continuous cycling of biological resources, the shift of organism species, and system adjustments that occur as a stream matures are today referred to as the river continuum concept (Vannote et al. 1980).

Each species has an optimum range for each environmental constituent. In that range, the species operates more efficiently. The more common and ubiquitous a species is, the wider the range of biological, chemical, and physical constituent conditions that are acceptable to the species. For example, there may be no perceptible change in organism performance between temperatures of 15.0 and 20.0 °C, but at temperatures above and below this range performance gradually decreases until the organism or the species no longer, can tolerate the conditions. These are not "go" and "no go" conditions, though the slope on reduced performance may be so rapid as to be unmeasurable, and thus they appear to behave this way. Fish may appear normal in water at near freezing temperatures, but continual exposure to such temperature would affect survival, because the fish may not be able to grow, mature, or reproduce. Many species are rather resilient to short-term adverse environmental conditions through many mechanisms built into them for survival, such as fatty food reserves, dormancy periods, and accumulation of physiological debts. An invertebrate species may disappear from a stream for periods of time; the species may be in an adult terrestrial phase of its life cycle, or the entire gene pool may be stored in microscopic dormant eggs that will hatch when conditions are optimum.

Tolerable ranges for common potentially adverse constituents have been compiled (EPA 1976), but for individual species and for many uncommon materials we lack knowledge and must assume that if the species is living in a river at commonly found numbers the habitat constituents are optimum or near optimum. Liebig's (1840) "law" of the minimum states that the amount of growth is limited by the material that is in shortest supply. Liebig was speaking in terms of chemicals or elements that serve as plant nutrients, but it is possible to expand the concept to other factors, such as light and temperature. We must bear in mind that the shortage is relative to its need. Phosphorus is referred to as a limiting nutrient in the aquatic environment, and much of this reference is based on our knowledge of a technology to control its entry into waterways and thus making it limiting. Algal cells can extract phosphorus from water until its concentration is reduced to only a couple parts per billion (micrograms/liter). The efficiency of recovery diminishes as the limiting concentration is approached. Growth may occur even after the concentrations become limiting, thus, we must recognize that some materials can be stored from periods of abundance to be used during periods of shortage. Until environmental concentrations approach or reach the minimum support values the quantity of material has little consequence on the well-being of the population of organisms. Some other material or factor becomes the population limit control. Plants may become so dense that they shade each other and thus light becomes limiting. To compensate for light shortages plants may develop more chlorophyll or photon interceptors.

Zinc, a micronutrient required by many life forms, when present in excess quantities could reach concentrations that are toxic to the same organisms it nourishes. There is a limiting maximum amount of many materials. Shelford (1913) expanded Liebig's (1840) concept to add maximum values to the minimum concept to formulate the "law of tolerance," or a tolerable range of life conditions. In environmental management we are fortunate to be concerned usually with only one end of the tolerance range. "Quality Criteria for Water" (EPA 1976) lists limits for zinc to protect aquatic life from toxic affects, it does not establish an amount that should be present to support the micronutrient needs of the waterway's life. It is nearly always naturally present so we need not worry.

There are many types of organism and population control factors. Chemical, physical, and biological factors are convenient categories. Familiarity with environmental data indicates that most of the cause/effect information falls into the physical and chemical categories. Biological criteria are coached verbally or are generic in character. Biological induced stresses are much more difficult to assess. The predator-prey relationship is a yes or no situation for the individual organisms involved. Can trout control the well-being of a caddisfly species? If caddisfly prey is in short supply will it stress the trout population? How much? Is it significant? Will it be more expedient to shift to mayflies and stoneflies rather than select the diminishing numbers and increase the effort to catch caddisflies? Will a trout move to "greener pastures"?

Balanced communities are the communities that man wants. An unbalanced community is composed of organisms we do not want or consider less desirable. An aquatic ecosystem of carp (Cyprinus carpio) feeding on sludgeworms nourished by sewage solids is balanced for conditions present just as much as the algae, minnow, bass community is, though the public prefers the latter. In the first situation, we have a wastewater aquaculture system living on and using the wastewater energy and nutrients; in the second we have a sunshine/photosynthesis based food system. We do not consider carp a useful product, though they are the best users of the polluted water and eventually help produce clean water. The predominant and dominant organism species will shift rapidly (weeks) as environmental conditions change to establish a new balance to best use changing and new conditions. If a stream's temperature rises to the detriment of native trout it will also be detrimental to some of the cold-water-loving plants and invertebrates. In a short time, organisms tolerant of and better adjusted to the new temperature regimen will occupy the vacated trout spaces and a new balance is struck, making bass consumers happy and trout consumers complainers.

THE HABITAT OF FISH FOOD ANIMALS

BOTTOM SPACE

The total quantity of benthic organisms present in a waterway must be governed somewhat by the quantity of bottom space. A lake of 80 surface acres has only slightly more than 80 acres of bottom for colonization and use. The slope of the bottom increases area so slighty that it is negligible. A stream segment 40 feet wide and 1,000 feet long would have 40,000 square feet of surface, or almost an acre. The slope of the bottom from the water's edges to the channel or deepest point would result in a measurable increase of the water-bottom interface to something above that of the level surface area. This water-bottom interface is the hydrologist's wetted perimeter (Figure 2). The wetted perimeter area is estimated by:

$$A = L \times \frac{a}{w} \tag{1}$$

where A = area of bottom-water interface or wetted perimeter

L = length of stream reach considered

w = width of the stream

a = area of the stream's cross section

If mean depth (d) is known, then $2d + w$ = an approximation of wetted perimeter. (Note: $a/w = d$.) Several cross sections representing the stream reach need to be surveyed. The channel continuously changes morphology throughout the reach. There will be deep areas with low water velocity and shallow areas with rapid water velocity. The wetted perimeter area will be greater in the subreaches with deep waters (pool) than in the shallow or riffle areas.

Wetted perimeter is much more important for hydraulic considerations than for biological studies. The wetted perimeter of the channel affects the amount of drag or friction on the over-passing water mass and thus, in part, governs the current velocity or time of travel of water. The nature of the bottom substrates, presence or absence of aquatic vegetation, and submerged cover materials have much more influence on fish food production than changes that may occur in the quantity of wetted perimeter area. To complicate matters, wetted perimeter changes as the flow of the river fluctuates. If there is an increase in discharge, formerly dry banks are submerged to become a portion of the wetted perimeter. This new aquatic area is subject to

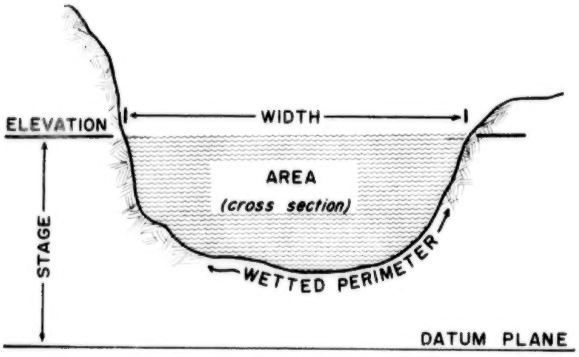

Figure 2. Stream channel components.

colonization, but time is required for migration into the new frontier by the invertebrates. Simple migration will not increase the standing crop of organisms, because migration involves only vacating one space to occupy another. Reproduction and growth are required to produce individuals and increase biomass to occupy all available niches.

A decrease in flow or discharge effects a reduced stage (surface elevation) and exposes former stream bed. Benthos occupying areas that will be exposed must migrate with the the receding waters or perish. Most fish food organisms have limited locomotory abilities. If there is sufficient time available for migration, there must also be unoccupied space available for them to move into.

Changes in wetted perimeter above some permanent or reliable base flow would have only a minor impact on the fish food production capacity of a stream. River currents could aid immigration into recently inundated bottom areas where physical habitat and food is likely available, but the immigrants would be stranded when the discharge and stage receded.

An increase in stage to above bank full forces water to flow over the flood plain. Organisms dislodged from channel substrates tend to return to the bottom within a short distance, but there is reduced opportunity or ability to return with the higher velocity currents associated with increased discharge and stage. Organisms drifting over the flood plain areas find reduced currents here and a better probability of negotiating a return to the bottom. Flood plain substrates might be adequate habitats for many forms, but when the flood recedes it is a great distance back to the permanent stream channel, and many

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may be trapped in temporary pools where they will die for a lack of currents or drying of the pool. Rivers subject to frequent flooding, such as southeastern coastal streams, contain a large number of species, but these have low populations. Intermittent flooding probably contributes to a low number of individuals per species through heavy loss of individuals swept onto the flood plains.

SUBSTRATE

A student of streams soon learns that the wetted perimeter is a complex surface varying in composition and roughness that is dependent upon the size of the substrate material. Sand and finer particles produce a smooth-bottomed channel. Substrate configuration can vary up to very rough boulders and even bedrock with varying degrees of complexity. Stream velocity and substrate composition affect each other. A smooth bottom supports laminar flow and swift velocities. The flow becomes more turbulent as the roughness of the channel increases. With the presence of large rocks, boulders, and other objects in the channel, the turbulence produces a visually impressive reach of fast water, but velocities may be reduced. There are micro areas with very swift downstream currents, but there are also micro areas of eddies and swirls where water is temporarily moving upstream, and some pockets of water may have little or no current.

Currents contribute to the nature of the stream bottom by sorting, transporting, and grading the material. A reach of cobble or boulder substrate has had the finer materials transported away, and these fines were deposited in areas where currents subsided or were transported out of the basin. Deposition occurred where the river no longer had the energy to transport gravel, sand, and other small particles. Particles of varying sizes derived from the same mineral material will have the same volume to mass ratios (specific gravity), but the surface to mass ratio is much greater on the smaller particle. The greater relative surface area has more friction with the water, and the increased tractive force allows the water to more readily move the smaller particles, either by rolling them along the bottom (bed load) or picking them up for transport (suspended load).

A boulder strewn bottom is not composed solely of boulders. Spaces between the boulders are filled with finer material of assorted sizes, including organic detritus that would take very little current energy to dislocate and transport. Eddies or quiescent areas behind and between the boulders allow settling and deposition of the fines to fill the interstitial spaces.

A cobble covered area has more effective water-bottom interface than a smooth sandy area. About half of each cobble is embedded into a substrate matrix composed of various sized particles; the remaining half extends upward in the water cross-section. This protruding "half-sphere" adds considerable bottom-water interface surface suitable for fish food animal occupancy.

The smaller a particle the more surface area per mass, an important consideration for chemical and microbial action. Small sized particles are a detriment to most crawling and anchoring animals. The particles are not stable and the addition of an animal's low mass but high surface area extending into the current magnifies the instability. For burrowing forms that move themselves into the substrate, fine particles can be an important habitat consideration. A substrate composed of a mixture of fine materials also has textural properties. Texture contributes to the stability of the soils. There may also be cohesion between particles. Worms (Tubificidae) bore into soil and assemble vertical tubes in which they live, head into the substrate feeding on organic material incorporated in the soils. The posterior end extends up into quiescent water and fecal pellets accumulate as a mound around the burrow. Burrowing mayflies (Hexagenia and Ephemera) build shallow, U-shaped, horizontally oriented tunnels. The soil must have cohesive qualities to prevent collapse and minimize maintenance while the nymph pumps water through the burrow to maintain oxygen and food supplies.

Many species of fish food organisms "view" the substrate particles as attachment sites, objects to hide under (interstitial spaces), or to crawl over (surface area with anchorage). The best combination of variety and number of organisms occurs in the areas of coarse gravel to cobble (Figure 3), or where the currents have sorted the substrate to this consistency. These areas also tend to hold a wide variety of species because of the many different microhabitats present. The interstitial spaces are filled with varying grades of material and pockets of substrate can be found for even quiet water forms such as worms. Benthologists tend to perform many of their investigations in these areas because of the numerous species present and the high numbers of organisms per unit area, characteristics that contribute the most information per unit of effort.

Sands and fine gravels are of little value as substrates for benthic animals. Few species and low numbers of individuals inhabit these unstable areas. Slight changes in flow, either increasing or decreasing, effect shifting and repositioning of these substrates. Animals present can have their substrate scoured from beneath or around them, are plagued by a near constantly rolling underfooting, or must combat burial by newly deposited material. Attaching animals need particle pieces large enough to grasp or serve as anchors, and the positionally unstable sands and fine gravels meet neither criteria. These areas offer no concealment for the wandering or grazing nymphs from fish or other predators. Shifting substrates are as hostile a habitat as are terrestrial sand dunes; in fact, ripples and dunes form in sand bottom stream beds. These are not much different than terrestrial sand dunes. They behave in the same way and the formation physics is the same whether the driving force of formation is a prevailing wind or flowing water.

Sands and fine gravels are not suitable for burrowing forms. Wiley (1981) found that areas where sand particle sizes equaled the width of a chironomid larvae head capsule were the most difficult site for a larvae to find a spot to burrow into and it took the longest time to prepare a burrow if a site was found. The species studied were those of the limited number of insect forms that favor the sand habitat. When sand and head particle size are the same the interstitial spaces are smaller than the larvae thereby preventing "worming" as could happen if the particles and spaces were larger. Removal of particles to excavate a burrow when the particles were the size of the organisms head certainly would be a formidable task when the only tool available to the larvae is its mouth. Larvae on this size substrate were also

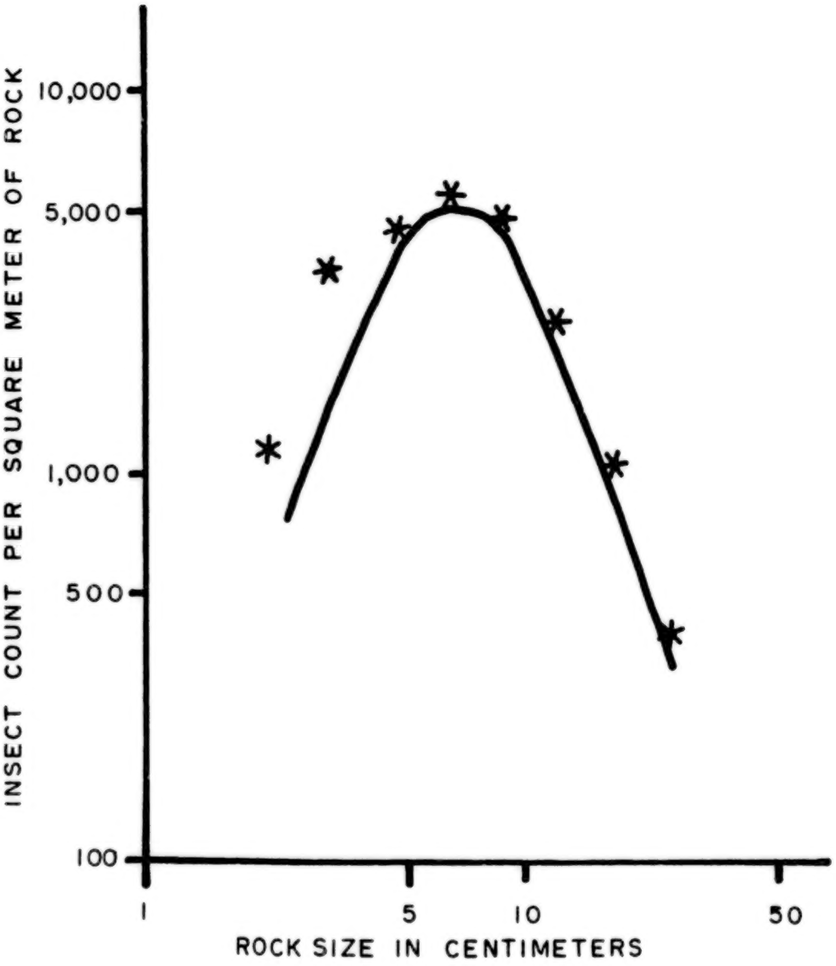

Figure 3. Effect of rock size on the number of insects per unit area of stream (modified from Lium 1974).

more susceptible to being swept away by the currents before finding a site or completing the burrow. This may explain why different instars (sizes) occupy different sizes of these fines.

Pools and other areas of low velocity are settling points for the fine sands, silts, clays, and organic detritus. These areas are relatively stable compared to the sand in the river run areas. Water-logged soils are composed of mixtures of particle sizes and composition. They exhibit strong cohesive properties based on the physical characteristics of the particles and the surface tension imparted by the entrained water. Clay stream beds can be nearly as compact and stable as bedrock. At the opposite extreme can be pockets of flocculant material composed principally of organic detritus. Some soils have large numbers of microbes, decomposing organic fractions, entrained in them, and the living organisms can impart a gellike consistency to the soil. Sludge beds are areas where sewage or other waste solids have settled

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and are a dominant component of the substrate. They vary in texture and stability, but have a distinct odor of decomposing sewage imparted to them by intermediate decomposition byproducts of residual proteins. Decomposing leaves, bark, and sawdust will not have the sewage odor, their odor may or may not be that of molds. Rich organic deposits can be substrates and food for many aquatic worms (Tubificidae). If the deposit is undergoing very rapid decomposition, gases (including toxic ones) are generated and can effect a boiling action in the mass. This instability prevents even the most tolerant of macroinvertebrates from establishing and maintaining themselves. If fibrous material is present, gas can be entrained and masses can become buoyant, floating to the surface and persisting until the gas escapes or turbulence breaks up the structure and the materials settle back to the bottom.

An aid in characterizing the bottom soils can be their feel when wet:

slick = clay
smooth = silt
gritty = sand

The variety of organisms found in bottom soils is usually less than found in the rock riffles of a stream. The basic reason for this is that the habitat is uniform in nature over extensive areas, the wide variety of microhabitats or niches is absent. But, limited kinds of clams, worms, snails, and burrowing larvae and nymphs can be present in tremendous numbers and biomass (standing crop).

Rather detailed substrate/soil analyses can be performed (Weber 1973). These can involve drying and grading with sieves, ashing to determine organic content, etc. Simple descriptive terminology is usually adequate for fish food resource evaluation. A number of indices or scales have been developed; the most widely used are presented in Figure 4. The Forest Service system is used by the U.S. Fish and Wildlife Service in physical habitat studies and appears to be quite functional, but it was designed for fish habitat with no provisions for soil or small particle characterization. Cummins (1962) and Wentworth (1922) classifications extend into the small particle classifications. None of the particle verbal descriptions deal with mixtures. The U.S. Department of Agriculture diagram (Table 1) provides terminology for various soils. Bovee (1982) suggests using a numeric code based on the Forest Service index when describing mixtures of large particles or objects. This code is required for computer modeling and projections but also has merit in that it can be translated readily to a verbal description. The first digit or word describes the dominant particle size. The second digit describes the prevailing subdominant particle size that fills the interstices between the dominant particles. For example, 72 would be large cobble bedded in small gravel. The substrate determines the forms of fish food organisms found and, to a lesser extent, how many. Substrate information supports the quantitative and qualitative fauna data and is an indication of how representative of the stream the data are. Cobble riffles may be representative, important fish food production areas in some streams, but they would be of little value if they occurred once or twice in a stream that was essentially all deep runs with soil substrates.

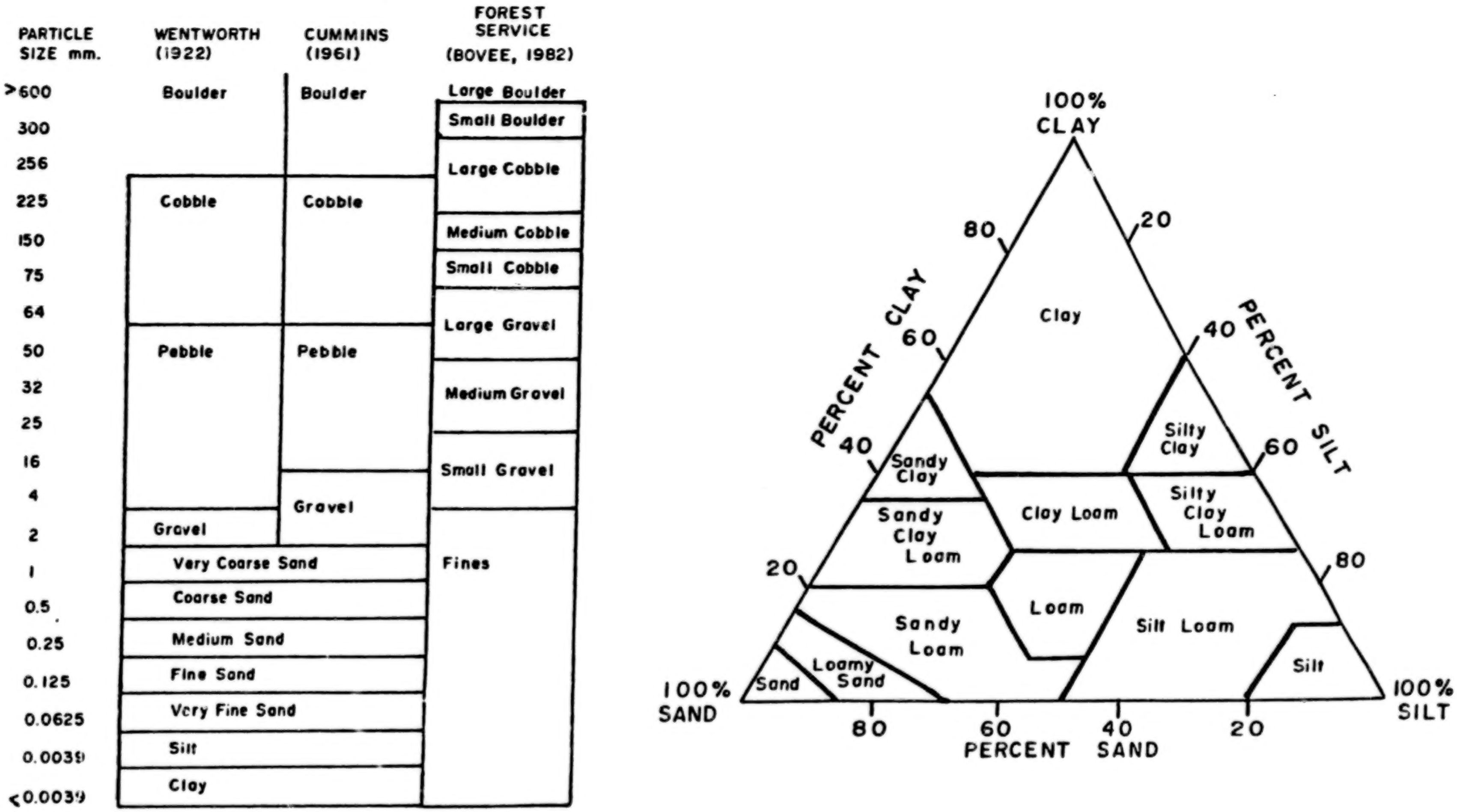

Figure 4. Wentworth, Cummins, and Forest Service soil or particle classifications. The diagram is the U.S. Department of Agriculture textural classification of soils (modified from Millar and Turk 1951).

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Marl (= tuff, tufa, or travertine in European literature) is a calcium carbonate deposit on or in the substrate. In hard (calcium carbonate saturated) water the material remains in solution with a complex chemical equilibria between carbon dioxide, the bicarbonate, and the carbonate ions. Loss of carbon dioxide through either aeration or photosynthesis by the waterway's plants effects a change in the chemical equilibria, with the bicarbonate concentration decreasing and the carbonate concentration increasing. When the carbonate concentration reaches saturation precipitation occurs. In lakes where plankton photosynthesis effects the precipitation the carbonate is a fine floc suspended in the water, and it can impart a milky appearance or light turquoise color to the lake's water mass. In marl streams, plankton is a minor component of the photosynthetic community, which is dominated by sessile attached algae and higher aquatic vegetation. Precipitation usually occurs first in benthic microhabitats, principally the geologic substrates that are covered by photosynthesizing algal cells (periphyton or aufwuchs). Marl deposits can be highly varied in texture ranging from slurries to solid cemented accretions. They can effect the formation of conglomerates composed of cemented rocks, incorporated organic debris, mineral fines, logs, and the photosynthesizing aquatic vegetation, originally the basis of the generation of the deposit. Chara, a macroscopic alga, is common in marl streams as dense beds of vegetation; it generates, in part, its own substrate of organic and mineral debris mixed with marl precipitates. This "soil" can be an excellent substrate for many burrowing animals, and many others colonize the Chara fronds.

There are nonmineral objects in a river that serve as excellent substrate for fish food organisms. A log jam is a virtual maze of surfaces. A fallen submerged tree has its many limbs covered with scurrying immature insects. Wood serves as attachment sites for many larvae that lead a sedentary attached life. A wood maze protects from excessive current velocity yet there is movement of water that circulates nutrition to the organisms. Shelter and concealment from foraging fishes is provided, but there is a constant loss of individuals due to mistakes and conflicts between the individuals of a growing population competing for the limited space available. Swept from cover and protection, the animals are vulnerable to fish waiting at downstream feeding stations.

Benthologists recognize the importance of this substrate, but do not have the technology to quantify the amount of habitat or the quantitative sampling tools to collect a known portion or quantity of a fallen tree, brush entangled snag, or beaver dam. Recent information generated by foresters for forest fire hazard evaluation allows calculation of the quantity of total tree wood or residual slash after loggers have completed their harvest. A method for calculating the surface area of a tree from weight and morphology data is presented in Appendix A. Results for three typical trees, 12 inches in diameter at breast height, and the various size classes of their branches and foliage are presented in Table 1. A newly fallen tree has much surface area for occupancy by fish food organisms and for the colonization of periphyton or aufwuchs that feed the animals.

The fallen and submerged Douglas-fir for which the surface area was calculated in Table 1 has about 0.13 acres of surface for occupancy by aquatic

Table 1. The surface area of various parts of Western trees (data in sq ft).

Branch sizes (inches)	Douglas fir	Western red cedar	Lodgepole pine
Foliage	4844	????	2367
0 - 14	489	253	480
¼ - 1	167	179	118
1 - 3	23	48	18
>3	0	0	0
Bole	98	79	117
Total	5621	559 (+ foliage)	3100

organisms. Eight of these trees per surface acre of water would double the amount of space over the regular bottom surface. With time, the finer fractions of the tree's structure disappear through processes of erosion and decay, but the bole and substantial limbs may persist for decades. These surface computations are for a "smooth" structure, but a newly fallen log has many nooks and crannies in the convolutions of the bark. With time, the bark loosens and fractures to create space between the bark and wood. Many nymphs and larvae thrive in these crevices. Eventually, the bark is eroded or sloughs off, but the log continues to differentially decompose. Knots and other rosinous sites decompose slower, and a log becomes more irregular in shape (irregularity in shape increases surface area). Rapidly decomposing portions of the log become spongy and fibrous, excellent sites for larvae to worm into.

Large quantities of information can be garnered from a submerged mass of wood by an experienced investigator. Though we lack the technology to quantitatively sample the substrates, the logs are covered with fish food organisms. If a log is left out of the water for a short period of time many species of nymphs and larvae, at first unseen, will be found crawling out of the drying cracks and crevices to seek water. In rivers with fine gravel, sand, and other shifting bed materials, the principal site for invertebrate fish food organisms will be the trees, logs, and brush that fell in or were washed in from the riparian lands bordering the stream.

The rooted large aquatic plants are an excellent substrate for fish food organisms. Plants will grow wherever there is a substrate that will permit rooting and where currents are moderated enough to provide bottom stability and lack the force to uproot the plant. Of course there must be sufficient water clarity to permit light penetration for growth and propagation. Excepting bedrock and coarse-bottomed mountain streams, unstable bottom streams subject to frequent floods or spates, and turbid streams, most of the Nation's rivers support extensive beds of rooted aquatic vegetation. This vegetation can be present in large quantities; an 18 mile reach of the middle Potomac River, Maryland-Virginia, supports 26 tons per mile of rooted aquatic plants in late summer (Keup and Hicks 1978).

Stems and leaves of plants provide excellent surfaces for occupancy by a multitude of fish food organisms. There is a many-fold increase in effective habitat area over the original stream bottom. These are aquatic high-rise apartments and as with humans living in apartment towers many more inhabitants per acre will be found. They also provide cover and concealment for the organisms. Plant surfaces are found covered with microscopic plants and animals that are the food for the grazing and foraging invertebrates.

Though long recognized as an excellent substrate for macroinvertebrate production, aquatic plant colonies are rarely studied by researchers. The following factors may contribute to this.

1. Most fish food studies have been done on trout streams, with reliance on samples from riffles. Mountain trout streams have little habitat for aquatic plant production.

2. Quantitative sampling technology is limited, and the quantity of vegetative material to be searched for organisms is much more than for rock substrate per unit area sampled.

3. Beneficial aspects of aquatic plants are not recognized by many persons. They are referred to as "weeds," which are to be destroyed because dense and extensive stands interfere with many physical uses of the water.

Harrod (1964), studying macrofauna on vegetation in the River Test, England, found most species segregating themselves from other species on various portions of the plant, and there was a seasonal fluctuation in abundance (Table 2).

Table 2. Seasonal variation in density of macrofauna in the River Test, England (organisms per 1,000 cm^2 of stream bottom = 1.08 ft^2).

Species of plant	Organism numbers (range)	Species found	Month of maximum number
Ranunculus fluitans	101-4690	31	January
Callitriche playtcarpa	75-369	45	October
Carex sp.	103-1916	25	January
Veronica beccabunga	58-288	29	October

Krecker (1939) related invertebrate fauna to plant stem lengths and found that the plants with the more complex structures (branching and leaves) had the highest density of animals. Seven plant species were studied, of which, Vallisneria spiralis had about three animals per foot of stem compared to the most complex plant, Myriophyllum spicatum, with 144 animals per foot of stem. Witcomb (1963) observed longitudinal distribution of animals by species along the plant fronds as well as numbers of specimens and variations of distribution at different seasons of the year. She also presents evidence that certain plants may attract some species and repel others because of chemicals secreted by the plants. Niesblowski (1980) also reported segregation along the fronds by major groups, with snails (Gastropoda) near the base, various orders of animals segregated along the midreach, and black fly larvae (Simuliidae) near the tips of the plants in areas where the currents were swiftest. With posterior sucker attachment, the filter-feeding black fly larvae can maintain position in the currents, while collecting food in cephalic fans. In August, as many as 340,000 black fly larvae and pupae were found per square meter (31,500 per square foot) of river. Tarzwell (1936), reporting on the results of installation of stream improvement devices, concluded that when currents were slowed and siltation occurred in backwater areas behind the improvement structures there was an influx of aquatic vegetation. These areas had the highest fish food production per unit area of stream when compared to other types of substrates evaluated. His results are summarized in Table 3.

Chara beds in a Michigan trout stream supported five times the biomass per unit area than that found in gravel/rubble riffles of the same stream (Keup 1958). These Chara stands carried at least 48 species of invertebrates, many of which were large, highly desirable fish food organisms such as stoneflies (Pteronarcys pictetti), Odonata nymphs, hellgrammites (Chauliodes spp.), and burrowing mayflies (Hexagenia recurvata and Ephemera simulans).

In temperate climates, rooted aquatic vegetation is seasonal; most of it is present during a period extending from late spring to early autumn. This temporary expansion of total substrate for fish food production coincides with the principal period of fish feeding and growth. Thus, aquatic vegetation provides space and food supplements for invertebrates when this demand as food by fish is greatest.

A number of plants float on the surface with roots suspended downward into the water column. Water hyacinths (Eichornia spp.) commonly overgrow much of the surface of subtropical and tropical waterways. They have substantial masses of roots that hang down into the water to secure nutritional materials for the plant. The root mass is covered with a jellylike mass of microscopic plants and animals and contains considerable quantities of plant detritus. The entire matrix provides food and shelter for considerable numbers of fish food organisms.

When a stream undercuts a river bank, clusters of roots from riparian vegetation are exposed and hang into the water. These mats and tangles support periphyton and a large biomass of fish-food animals.

All of the previously mentioned substrates are subject to modification through overgrowth of biological films (periphyton or aufwuchs). Within a few

Table 3. Density of macrofauna associated with stream bottom substrate and vegetation (Tarzwell 1936).

Substrate type	Per square foot of bottom Organism volume (cm^3)	Organism number
Rubble	3.81	243
Gravel and rubble	6.56	1221
Coarse gravel	4.24	555
Medium gravel	4.07	466
Fine gravel	1.15	52
Moss, gravel, and rubble	18.10	4535
Moss on medium gravel	14.25	357
Moss on fine gravel	11.62	728
Sand and gravel with plants	8.74	743
Gravel and silt	1.85	33
Gravel and sand	2.07	190
Sand and silt	1.62	73
Sand	0.13	2
Chara and silt	3.58	126
Muck, sand, and plants	8.15	706
Elodea beds	58.00	1896
Watercress	39.22	2233
Ranunculus	24.13	6750
Vallisneria	19.62	1766
Potamogeton pectinatus	3.17	59
Chara	5.94	290
Potamogeton filiformis	5.63	876
Mucky flats	5.05	217
Marl	0.70	69

days, a substrate exposed in water will be colonized by bacteria, diatoms, other algal cells, and microscopic animals. Rocks in the most infertile, cold mountain streams are yellow-brown colored and have slick surfaces that are due to these overgrowths. Under conditions of good growth, streamers of attached filamentous algae may wave in the current. These streamers are expanded substrate and are colonized by many larvae and nymphs. Thick mats (to over 1 cm thick) of periphyton may overgrow extensive areas of stream bed and drastically alter the natural configuration and composition of the substrate at the bottom-water interface. Insect larvae and worms will thrive in this food source and burrowing medium. If the mat grows thick enough, the bottom cells that anchor the mass begin to die because of old age or a lack of light or nutrients caused by burial with the newer upper growth. Death and decay of these base cells weakens the attachment and facilitates the river currents sloughing off patches of material. Death and decay of bottom layers of cells also results in the production of decomposition gasses that tend to be entrained at the bottom of the jellylike mat. Photosynthesizing surface algal layers of the mat produce oxygen bubbles within the mat. Either or both sources of entrained gas result in increased buoyancy and pieces of the mat break loose, sometimes with substrate fines still attached, and float downstream carrying an entrained colony of animals with them.

Quantitative sampling of many substrates cannot be performed because of the absence of tools. Surber and similar samplers (square foot), grabs, and dredges (Weber 1973; APHA et al. 1980) are limited as to the configuration and nature of the substrate they will function in. Beds of weeds in shallow water can be sampled with Wilding or stove-pipe cylinder samplers, but rarely are because of the lack of interest or resources to separate animals from bushels of vegetation. There are no devices to sample areal or volumetric quantities of logs, tree tops, root tangles, and other superb habitat. Artificial substrate samplers are used in water quality studies to standardize the habitat and overcome adverse bottom conditions, but they can be misleading and not at all representative of the natural habitats. The standing crop in the unsamplable habitats can usually be expected to be greater than that found in the sampled riffles, runs, and pool areas.

Different mineral substrates yield different quantities of fish food. This has long been known to fisheries managers. Pate (1933) documented the different biomasses found in New York State trout streams (Table 4).

Table 4. Macrofauna biomass variability over stream bottom substrate in a New York stream (Pate 1933).

Substrate	Biomass of organisms (grams per square foot)
Silt	3.07
Rubble	2.47
Large rubble	1.55
Small rubble	3.55
Coarse gravel	1.51
Fine gravel	0.93
Sand	0.10

Tarzwell (1936) (Table 5) found similar results in Michigan streams, plus the fact that production in silted areas was further enhanced if vegetation grew there. Algal mats or streamer growth of algae will enhance the production of mineral substrates. Streamer growth on fine gravels may be a detriment

Table 5. The relative quantity of bottom animals per unit of substrate. Sand is the poorest substrate (Tarzwell 1936).

Substrate	Multiplication factor
Sand	1
Marl	6x
Fine gravel	9x
Sand and silt	11x
Gravel and sand	12x
Sand, silt, and debris	13x
Gravel and silt	14x
Chara and silt	27x
Potamogeton pectinatus	28x
Rubble	29x
Coarse gravel	32x
Chara	35x
Muck	35x
Medium gravel	35x
Potamogeton filiformis	43x
Gravel and rubble	53x
Sand and gravel with plants	67x
Muck, sand, and plants	67x
Moss on fine gravel	89x
Moss on coarse gravel	111x
Moss on gravel and rubble	140x
Vallisneria	159x
Ranunculus	194x
Watercress	301x
Elodea	452x

because the currents effect a drag on the streamers, which tends to dislodge the small pebbles causing instability.

Needham (1927) found bedrock areas of streams supporting the lowest standing crop of invertebrate animals; silt areas had the highest quantity (weight, no aquatic plants present). Ranked in order of standing crop his findings are summarized in Table 6.

Needham also found narrow streams to have the greatest standing crop of animals (<7 ft wide, 2.36 g/ft^2; >7 ft wide, 1.04 g/ft^2). Midstream areas of streams >18 ft wide had less organisms than were found along the shores of these streams; he did not speculate why. The smaller streams would tend to be nearer the headwaters, with steeper gradients and coarser substrates. The

Table 6. Biomass of invertebrates as a function of stream bottom substrate (Needham 1927).

Substrate	Biomass of organisms (mean grams per square foot)
Bedrock	.0065
Hardpan	.1
Sand	.46
Muck	.65
Fine gravel	.98
Average substrate	1.21
Coarse gravel	1.28
Rubble	1.88
Silt	4.29

larger streams would be farther downstream in the watershed and have lower gradient, less velocity for fines transport, and a greater load of fines because of the larger watershed source. (Lower gradients and land relief in downstream areas and the larger valleys would be more likely developed for urban and agricultural activities, both important sources of erosion-originated fines.)

Maintenance of coarse gravel and rubble substrate would appear to be a must for good fish food production. To maintain this substrate, there must be periodic spates to flush accumulated materials from the interstitial spaces, otherwise these areas will fill and the diversity of microhabitats will disappear. If substrates are subjected to burial by settled fines, either through reduced flows or increased sediment load, there is a drastic reduction in the kinds and quantity of animals that can inhabit the area (Tebo 1955; Bartsch 1960).

In 1970, I worked on the lower Missouri River, from Sioux City, Iowa, downstream. I found a paucity of benthos in the river channel where currents of up to 6 mi per hour (over 8 ft per second) maintain a shifting sand bottom. Benthic animals were common and abundant on the manmade rock dikes and rip-rap installed to facilitate navigation. Silted eddy areas around the wing dikes and brush-log collections near the bank also contained large numbers of invertebrate animals. Some persons might blame this lack of good invertebrate substrate in midchannel on efforts to channelize the river and to use the hydraulics to maintain channel integrity and depths. This is not so. The Missouri River has always been a swift stream channeled in a fine alluvium plain. Gravel and rubble are scarce, the soil sediment load is high, and the currents keep much silt and clay in suspension. Berner (1951) found a very short supply of fish food in the Missouri River in 1945, prior to extensive civil works for navigation enhancement. His data show that in mid-stream and at sand bars the biomass of terrestrial invertebrates rolling along the bottom and inadvertently collected in his quantitative dredging exceeded the aquatic forms (Table 7).

Table 7. Biomass of invertebrate organisms in the Missouri River (Berner 1951).

Sample site	Organisms (lb per acre)	
	Aquatic	Terrestrial
Near middle	0.01	0.20
Near steep bank	2.17	0.12
Near sand bar	0.67	1.42
Downstream of dike	1.27	1.30

These values are all extremely low standing crops. Accidental loss of terrestrial animals to the river contributed as much or more biomass to the fish food resource as was produced within the river channel. The addition of large rock rubble to construct wing dams and dikes and to rip-rap unstable banks probably has enhanced the river's fish food production.

Stream flows must periodically enter flood or spate conditions to generate velocities sufficient to flush fines from coarse substrate materials. These flows cannot have velocities so high that they scour or move the gravels and rubble. Moving gravel and rubble would grind the fauna and flora into near extinction. Very swift currents may leave only very large boulders and bedrock shelves, both less desirable substrates for fish food growth. Manmade stream improvement structures tend to funnel the flows through constrictions, where higher velocities scour deeper reaches and pools and keep sediments and fines out of the gravel and rubble of selected areas. Fines are permitted to accumulate in more quiescent areas near the shore of the old channel and behind structures. These areas can be extremely productive of vegetation, where productivity can be further enhanced.

Another alternative for fish food production enhancement may be to manage for lower velocities, which would permit the development of a soil or mud substrate. Reduced flows or a series of check dams would allow soil development. This could effect an ecological maturation of the stream. A highly productive community, but with less variety of forms, could develop in the substrates. This would be management to approach Gersbacher's (1937) description of a "climax" stream community of burrowing mayflies, clams, snails, worms, and midge larvae. The Illinois, Sangamon, Wabash, and similar rivers have benthos of this nature. The large navigation impoundments of the Ohio and upper Mississippi Rivers have slowed the water in many areas to allow sedimentation and the development of soils within the pools or backwaters. Management to this end product could probably not be implemented for a number of reasons.

1. Unless the stream were near this state already, there would be drastic changes in fish fauna. Fish fauna would shift towards bottom feeding forms, many of which are less used by sports and commercial fishing interests.

2. Slower-moving water would lengthen the time of passage through a reach, and water temperature would increase.

3. Slower water would permit more extensive growth of aquatic plants (both rooted and planktonic), which might interfere with several water uses, notably water supplies for domestic and industrial uses.

4. Slower, deeper water with lower aeration rates would complicate pollution problems from decomposing organic materials and wastes.

5. Hydraulic engineering problems could be insurmountable. Aggradation of the stream bed would increase the tendency of the stream to meander or cut new channels.

6. Flood problems could be enhanced in local areas because of a shallower channel. In fact, many streams at this state of maturity have been channelized in the name of flood control, but to the detriment of the fish and their food organisms. The new channel has less habitat and adverse substrates, usually barren sands.

FOOD FOR FISH FOOD ORGANISMS

Bottom fauna are consumers; they can be classed as herbivores, carnivores, or omnivores. More refined delineation of feeding modes may include terms such as filter-feeding, grazing, shredding, and detritivore. A frequent question deals with whether food is limiting to the development or well-being of invertebrate populations. It probably is not if we look at the collective invertebrate assemblage. Hynes (1972), in his monumental treatise "The Ecology of Running Waters," devoted less than a page to food as a factor controlling benthic invertebrates. Hynes (1972) said, "Generally speaking species occur, or are common, only where their food is readily available, but it should not be forgotten that few running-water invertebrates are very specialized in their diets. For instance, many insects can eat either algae scraped from stones, or detritus, and diets may change somewhat with season according to the availability of algae." Some aufwuchs or periphytic growths can overgrow an area to the detriment of some species, but this complex of animal and vegetable foods will favor other species. The net result will be a change in species found, but not necessarily a change in the number of different kinds found (some common species will become rare and vice versa), and a good likelihood of increased productivity (standing crop may be reduced, but the turnover rate of the new predominant species may be much greater).

If fish food organisms are present in reasonable quantities, one of the contributing factors to their presence and abundance is available food. A fish biologist, after finding fish in good condition, who then pursues a search for the food's food, would be undertaking a rather questionable pursuit, no matter how "interesting" his findings may turn out.

If fish food organics are in short supply, their food resources may be but one of many potential limiting factors. Assuming a 10 to 1 food conversion factor between the "links" of the food web, a minimum twofold increase in the food chain base would have to occur to double the invertebrate population. Since a number of macroinvertebrates are predators on other macroinvertebrates, there is still another food web "link," requiring a still larger primary food base. The result is that an increase greater than twofold, maybe as much as several fold, would be required to double the secondary and tertiary production. Changes of this magnitude in the primary food base are substantial and should be apparent.

Within the past two decades benthologists have undertaken numerous investigations into the feeding of invertebrates. The purpose of these studies was to better understand the trophodynamics of the ecosystem and, as such, the studies are rather academic to the production of fish. An invertebrate gut analysis may show a diet of 95% of a single species of algae, from which we might conclude this is a dietary requirement. It is probably more likely a combination of food availability and preference. Elimination or replacement of the algal species most likely would result in the invertebrate feeding on another species, again selectively. Only rarely are animal species found to be restricted to a single food item.

Aquatic invertebrates do have some specialized food requirements; they are not all omnivorous. Predators are selective; some prey organisms are too small to provide sufficient nutrition, and others are too large to cope with. Supply and accessibility must be factors, and there are definite feeding mechanisms. Some predators grab their prey, macerate them, and ingest the carcass tissues; others grab the body, suck out the juices, and then discard the carcass. Some herbivorous species may ingest small plants or vegetable particles, with or without masceration, while others chew bite-size chunks from larger plants, eat detritus, or bore into the plant, eating as they go. A few herbivores pierce the plant, sucking fluids from cells and tissues. There are parasites, some living on other invertebrates, others, such as some leeches, who forage periodically on larger animals. There are examples of symbiotic and commensal relationships for a few species. The invertebrate community is so diverse it exhibits every known feeding and life style. It is ubiquitous enough to fill and use every niche and flexible enough for species to expand their habitats to occupy a niche if it is vacated.

Literature dealing with macroinvertebrate foods and feeding frequently implies that the periphyton or aufwuchs, plankton, and detritus are only plant material. Aufwuchs is an assemblage of life forms, including many microscopic animals (e.g., protozoans, metazoans), along with a collection of microdetritus, bacteria, and fungi that are incorporated in the matrix. Filter feeders, using either their body structures or by constructing miniature nets to collect masses of plankton from the bypassing currents, may be limited as to the size of materials they can intercept and retain, but they certainly are not restricted to algal cells and vegetable detritus. Organisms that chew detritus or ingest sediments must ingest the micro-fauna and flora in or on these materials.

Table 8 summarizes the feeding process and foods of commonly encountered riverine macroinvertebrates. More detailed information on habitat, habits, and trophic relationships of aquatic insects is presented by Merritt and Cummins (1978).

A still unsolved and widely debated issue is whether streams have true plankton. Suspended plankters will be found in stream waters, but in the smallest streams they probably originate as material lost from the periphyton. In large rivers, there is little question that there is a plankton community. Blum (1956), reviewing the river algae, stated " . . . workers are generally agreed that no distinctive association of phytoplankton is found in streams, although there is some evidence of this for individual zooplankters and for a few individual algae and bacteria. Plankton organisms are often introduced in the current from impoundments, backwater areas or stagnant arms of the stream. . . . Rivers whose plankton is not dominated by species from upstream lakes or ponds are likely to exhibit a majority of forms which have been derived from the stream bottom directly and which are thus merely facultative or opportunistic plankters." In swift, turbulent streams, the more structurally complex plankters, especially the long-chained and other colonial algal masses and the microcrustaceans, are subjected to violent destructive currents. In slow-moving rivers, large numbers of these can develop, and they experience rapid population fluctuations and blooms when conditions for growth are ideal. In even the most infertile and hostile small streams, considerable numbers of filter-feeding benthic animals, such as black fly larvae and net-spinning caddisfly larvae, can secure adequate food. The food resources (some may be detrital) are suspended in the flowing water, and the question is moot as to whether the plankton originated as scoured periphyton or with inflows from quiescent backwaters, wetlands, ponds, or lakes.

Filter Feeders

Filter feeders capture plankton or seston that are suspended in the water column. There are two basic capture systems: (1) morphological adaptations, e.g., fringes of hair or fans that are spread to the flowing water (examples include some mayfly nymphs, black fly, and midge larvae) and the siphon pumping system of the clams; and (2) the spinning of nets in a variety of shapes and sizes unique to the species. This is common to many species of caddis larvae, which regularly clean the nets and ingest the captured food particles.

Morphological adaptations to feed on seston are best exemplified by the Simuliidae or black fly larvae. Fan-like structures are located on the head of the larvae and are spread to the current to capture microseston. These larvae can clean very small particles (to 0.09 microns), including colloids and bacteria, from the bypassing water (Wotton 1976). The bulk of their food is probably diatoms and detritus in the 10- to 100-micron size range (Elsen 1979). The larvae usually assimilate over 50% of the diatom biomass during a gut passage time of less than 1 hour (Ladle and Hansford 1981). Large numbers of black fly larvae can have a substantial effect on a stream's seston supply.

Table 8. Commonly encountered riverine fish food organisms, their food and feeding processes (insect data consolidated from Cummins 1973).

Taxonomic group	Common name	Predominant food	Feeding[a] process
Caenidae	Mayfly	Detritus and aufwuchs	S,G
Ephemeridae	Mayfly	Detritus and aufwuchs	S,G
Leptophlebiidae	Mayfly	Detritus and aufwuchs	S,G
Baetidae	Mayfly	Detritus and aufwuchs	S,G
Ephemerellidae	Mayfly	Detritus and aufwuchs	S,G
Heptageniidae	Mayfly	Detritus and aufwuchs	S,G
Siphlonuridae	Mayfly	Detritus and aufwuchs	F
Phryganeidae	Caddisfly	Macrophytes	C
Leptoceridae	Caddisfly	Macrophytes	C,G
Limnephilidae	Caddisfly	Detritus and aufwuchs	C,G
Lepidostomatidae	Caddisfly	Detritus and aufwuchs	C,G
Philopotamidae	Caddisfly	Plankton	F
Psychomyiidae	Caddisfly	Plankton	F
Hydropsychidae	Caddisfly	Omnivorous	F,P
Brachycentridae	Caddisfly	Plankton	F
Glossasomatidae	Caddisfly	Aufwuchs	G
Helicopsychidae	Caddisfly	Aufwuchs	G
Molannidae	Caddisfly	Aufwuchs	G
Odontoceridae	Caddisfly	Aufwuchs	G
Rhyacophilidae	Caddisfly	Annual prey	P
Polycentropidae	Caddisfly	Annual prey	P
Chironomidae	Midge	Varied by species	C,F,G,P,S
Ephydridae	Shore fly	Macrophytes	C
Tipulidae	Crane fly	Detritus	C
Simuliidae	Black fly	Plankton	F
Culicidae	Mosquito	Plankton	F
Culicidae	Phantom midge	Plankton	F
Ceratopogonidae	Biting midge	Detritus	S
Tabanidae	Horse fly	Aufwuchs	G
Rhagionidae	Snipe fly	Annual prey	Piercing for body fluids
Plecoptera			
Filipalpia	Stonefly	Macrophytes	C
Setipalpia	Stonefly	Animal prey	P
Hydrophilidae	Water scavenger	Detritus	S

(Continued)

Table 8. (Concluded)

Taxonomic group	Common name	Predominant food	Feeding[a] process
Dystiscidae	Predaceous diving beetle	Animal prey	P
Psephenidae	Water penny	Aufwuchs	G
Dryopidae	Dryopid beetle	Detritus	C
Elmidae	Riffle beetle	Detritus	C
Gastropoda	Snails and limpets	Aufwuchs	G
Pelecpoda	Clams or mussels	Plankton	F
Sialidae	Fishfly larvae	Animal prey	P
Corydalidae	Hellgrammites	Animal prey	P
Anisoptera	Dragonfly nymphs	Animal prey	P
Zygotera	Damselfly nymphs	Animal prey	P
Decapoda	Crayfish	Detritus	C
Amphipoda	Scuds	Aufwuchs	G
Isopoda	Sowbugs	Detritus	C
Tubificidae	Sludgeworms	Detritus	S
Hirudinea	Leeches	Animal prey parasite	P

Note: A number of invertebrate animals not listed above may be found in rivers or streams. Their preferred habitat may be standing water, but they can adapt to some stream situations. Other forms of animals are present in good numbers but are marginal fish food or are not usually included in fish food censuses. Examples of some of these animals are the planarians, several forms of water bugs, and the surface-dwelling, air-breathing beetles. The term aufwuchs has been deliberately used in lieu of the English term periphyton, which has a connotation of overgrowing plant life. The German term cannot be literally translated, but includes the animal, bacteria, fungi, etc., forms of microorganisms that compose this film of life overgrowing all submerged objects.

KEY: C = chewing or mining
F = filter or net gathering
G = grazing or scraping aufwuchs
P = capture and chewing animals
S = sediment ingestion

Evidence exists that certain species' life histories and abundance may be tied to seston influx from lakes and other lentic waters (Spence and Hynes 1971; Carlsson et al. 1977; and Hansford 1978).

Caddis larvae or worms, especially the families Philopotamidae, Hydropsychidae, and Polycentropidae, are builders of various types, sizes, and styles of nets. Extensive work has been undertaken on their distribution, microhabitat selection, feeding methods, food preferences, and ecological roles (Edington 1968; Wallace et al. 1977; Fuller and Mackay 1980, 1981).

Upper Mississippi River towns have long been plagued by nuisance quantities of adult caddisflies that emerge from the river. Three species compose the periodic mass emergences: Hydropsyche orris, Cheumatopsyche compyla, and Potamyia flava. The larvae live in distinct portions of the tailwaters of navigation dams along the river. The flowing waters deliver abundant seston that was grown in the quiescent waters of the pools upstream from the dams (Fremling 1960).

A few representatives of other insect orders also are filter feeders. Examples are Olioneuriella, Elaossoneuria, and Isonychia mayflies (Hynes 1972). Representative dipterans (true flies) are the genera Glyptotendipes, Polypedilum, Endochironomus, Rheotanytarsus, Tendipes, and Kiefferulus; all are midge larvae with various filter-feeding styles and modes (Oliver 1971).

Clams are filter feeders and are noted for the tremendous quantities of water they filter and the efficiency of extraction of suspended food, including bacteria. They generally are not considered fish food because of their large size and because few species of fish can macerate the clammed-up clam for ingestion. The finger-nail clams, Pisidium and Sphaerium, are smaller and are taken by a wider variety of fish. Adult pearl button clams, e.g., Unionidae, are practically immune to fish predation because of their large size. Large biomasses of clams are present in some rivers and represent the assimilation of tremendous quantities of seston over a period of several years. The atypical large size of the mollusks must be considered by a benthos investigator, since a single specimen can outweigh by several fold the combined mass of all the other invertebrate fish food organisms present in a quantitative sample. For fish food analysis they need not be considered unless you are concerned about molluskivorous fish.

Grazers

Another mode of feeding is bottom grazing on attached or sedentary vegetable materials. Many investigators separate this group into those that consume living periphyton and those that feed on dead or detrital material, but I agree with Hynes (1972): " . . . many such animals are remarkably unselective and they eat everything they can scrape off." Many detailed food studies show that the invertebrates graze on certain items or that certain items tabulate into high percentages or frequencies of occurrence. This is probably the result of those materials being predominant in quantity, availability, or accessibility compared to other materials. Little work has been done on the consumption of materials in relation to benthic community composition. If the material is of a size, composition, and texture for ingestion, it is probably fair food. A snail eating its way across a rock surface leaves a well cleaned trail, except for a train of fecal pellets, having gleaned all the aufwuchs in its path. Insect nymphs are not as thorough in their grazing, but there is little evidence that they require or seek out certain food items.

Within the past two decades there has been keen interest in the role of terrestrial detrital material (e.g., leaves, twigs, needles) in the economics of the stream's nutritional budget. Some investigators have become so enthralled with the concept that stream insects subsist on fallen tree leaves that they have made unwarranted statements to the effect that the stream's life is supported by riparian vegetation. There is little question that terrestrial input plays a role in the bionomics of a watercourse, but it is quite likely that this material forms less than half of the food base in nearly all natural streams. Autumn leaf fall contributes a large quantity of organic material as a sudden short-term surge at a time when the stream's primary production is decreasing in its annual cycle. These leaves are not consumable until they have undergone considerable mechanical and biological degradation. Emulsification and hydrolysis take a lot of time, and large quantities of leaves are swept from the stream and the insects' access during this time. Many months after their origin, accumulations of terrestrial detritus may be found in an untouched state.

The origin of detrital material consumed by invertebrates is usually not discernible and is often classed as various sizes of particulate organic material (POM). Remember that the autumn period is also a die-back time for the aquatic vegetation (both aufwuchs and macrophytes). Thus, this aquatic vegetation also contributes substantially to the POM pool. In fact, aquatic vegetation will more rapidly enter this pool because of the near lack of tannins and lignins. These are very resistant to decomposition, and are important components of terrestrial vegetation. Tannins and lignins are high-calorie carbohydrates that are not easily digested or hydrolyzed; they can be used by very few organisms, and then only at slow rates. They can and will resist degradation for centuries in lacustrine deposits. The aquatic plants are all more herbaceous and succulent, or contain high water concentrations (80%-90%), an important factor that aids in their consumption and facilitates rapid mechanical and biological disintegration.

A major function of the detrital resource pool may be its role in sustaining animal populations through periods of fresh forage shortage. Streams subject to frequent and rapid changes in discharge frequently have low standing crops and primary production rates because of the periodic loss of aufwuchs to scouring during spates. The detrital deposits are stored in the substrates' nooks and crannies and are subject to only minor losses during these spates, unless the currents are so strong that the bottom substrate materials are temporarily dislodged, which frees the incorporated organic materials for transport out of the stream reach. Detritus-filled crevices are also protected areas that are sought out and occupied by many fish food organisms.

Some authors separate from the grazing group a group called shredders. Shredders are capable of physically removing chunks of food from a large forage object, such as leaves on plants. They shred for food, not to prepare particles for other organisms or for protective case or dwelling construction. Some of the particles are probably inadvertently lost and then intercepted by other downstream species. These shredders are as much herbivorous as are the species that engulf and then ingest microphytes.

The aufwuchs assemblage contains microzoans, mycelia of fungi, bacteria, etc., and numbers of these are also ingested with the matrix of algal plant material. Macrophytes and detrital material contain an overcoat of aufwuchs. Though grazers are primarily herbivorous, they do inadvertently ingest organisms other than the predominant algae and plant material. They are analogous to the cow that consumes the slow-moving aphids on her alfalfa. If we knew more about invertebrate dietary and nutritional requirements, we might be surprised that certain essential materials are obtained from these atypical and adventitious appearing foods.

Compared to the terrestrial insect community, there is a remarkable shortage of aquatic species that bore and mine their way through vascular plant tissues, eating and digesting the tissue as they go. The reason for this may be that aquatic vascular plants are primarily annuals. Their lives and persistence are seasonal, and they would not provide the food, cover, and concealment found in the terrestrial community, where forbs and trees, living or dead, persist through many years or even for decades and centuries, thus providing a continuum of consistent and dependable habitat for the invertebrate colonies within them. Only few, relatively rare, genera of aquatic insect larvae exhibit this mode of habitat and feeding. These are primarily confined to emergent or semiaquatic vegetation, such as cattails (Typha spp.), rushes (Juncus spp.), and water lilies (Nuphar and Nymphaea spp.). A debate could be sustained as to whether most of the plant host species are aquatic or terrestrial. Most of the colonized plants are perennials, a minority life-style for aquatics, but one that will assure a continuum of habitat from year to year. The fish food investigator can view most of these few species academically.

Considerable quantities and variety of invertebrate animals can be found in the mechanical and decay-developed cracks and fissures of woody objects. Many species like or prefer to occupy the space that develops between the bark and wood of a submerged log, but they use this space primarily for cover and concealment. They rely on circulating waters to bring in food, or they go out and forage. There are few species that diet on the decomposed wood fibers within these spaces.

A single pass of material through an animal gut, followed by decomposition of the animals' feces to the chemical nutrient pool of the ecosystem, is not the mode in nature. Since there is unassimilated energy and nutrients remaining in the fecal material the potential for use is there, and it is taken. The aquatic invertebrate community has its "dung beetles." Minckley (1963) found that sowbugs (Asellus sp.) in a small Kentucky stream were primarily dependent for their food on the feces of a scud (Gammarus sp.). Some species of mayflies ingest feces directly from their own anus as well as feeding on detritus (Pleskat 1953). This is not a weird phenomenon, it is common among mammals to consume the feces of other species and at times their own, especially when cleaning the nests of their young. This supports the view that organisms feeding on detritus are facultative in their food consumption, eating anything organic that they encounter and can ingest. Optically and chemically, it would be a difficult task to separate a slightly aged insect fecal pellet from a miniature gob of leaf mold or detritus. Scatophagy is one of nature's ways of conserving materials, nutrients, and energy. To decompose fecal material back to mineral plant nutrients and restart the food chain would be inefficient.

Sediment Feeders and Burrowers

This group has been less studied in streams than in lakes. The reasons may be that "worms" are probably the most commonly encountered members of lake habitat, and worms rank among the lowest forms of life on either the aesthetic or romantic scales of the benthologists working in the more varied fauna of streams. It is only within the past decade that serious efforts have been put forth on the taxonomy or identification of the many species of true worms (Oligochaeta) found in North America.

In addition to the worms, there are several groups of Diptera larvae, some fingernail clams, burrowing mayflies, leeches, Cladocera, Copepoda, Ostracoda, nematodes, planarians, and occasional horsehair worms that are intimately associated with the soils of waterways. They live within the soil, ingesting it and associated organic particles that serve as their food.

An old rule-of-thumb for a good fishing stream is 50% riffle areas and 50% pool areas. A river's soils are primarily the substrate of the pools, and it is in this habitat that sediment-associated organisms will flourish. Lesser numbers will also be found in samples from riffles, where they occur in the soil pockets filling the interstices of the coarser substrates. Using a 50/50 riffle/pool criterion, half of the benthic space in a good fishing stream will be habitat where the burrowing forms are prevalent. In America's largest rivers and in most prairie, agricultural, urban, and other low-gradient waterways, the pool reaches exceed the riffles, or riffles are very scarce to not present. It is safe to say that the low-gradient, primarily pool, streams contain a greater biomass of sediment dwellers than any other class of invertebrates. Fish food samples from these areas will contain a lower diversity of species, but the numbers of individuals and the biomass per unit area will frequently exceed by several fold the quantities found in samples from equal areas of riffle habitat. The numbers of worms in rich organic sediments can approach incomprehensible numbers. The Oki River in Russia has areas with up to 640,000 one-third inch long worms (*Proppus volki*) per square meter (Neizvestnova-Shadina and Lyakhov 1941). Populations of tubificid worms of approximately 450,000 per square meter [or about 1 kg (2.2 lbs) per square meter of bottom] have been found in Chicago area canals and the Little Calumet River, Indiana (Keup et al. 1965).

Oligochaete worms usually burrow vertically into the sediment for a distance of several inches. A posterior fraction of the worm extends upwards into the water. The animals ingest both mineral and organic particulate materials. Gut contractions use the mineral particles in a gizzardlike action, aiding grinding of organic particles to facilitate digestion. The upper opening of the burrow is surrounded by a cone of fecal pellets. The worms feed continuously. Based on Purdy's (1930) observations, they have a gut passage time of about 45 minutes, during which time they reduce the organic content of the muds about 60% (based on biochemical oxygen demand reduction between the raw mud and the fecal material). These are the manure worms of aquatic ecosystems. To a point, they will increase their populations in response to increased organic material, and abundant standing crops serve as indicators of organic pollution in waterways (Keup et al. 1966; Mackenthun 1969). Dense populations can impart a pale pink or rosy hue to a bottom, which suddenly disappears when a shadow is cast or vibrations from a footstep frightens them and they retract into their burrows.

There are a number of midge larvae (Chironomidae and Ceratopogonidae) that live in muds and fine organic materials. Many crane fly (Tipulidae), phantom crane fly (Ptychopteridae), and horse fly (Tabanidae) larvae are also mud substrate animals. These all have an affinity and need for the substrate and its food value. They are also tolerant, in varying degrees, to the environmental constraints of low dissolved oxygen and high concentrations of decomposition products found in organic enriched soils with relatively poor water exchange or circulation. Many of these burrowing organisms are equally at home in the thick matrix layer of algal growths or aufwuchs that overgrow stream bottoms in many areas.

Not all sediment feeders and burrowers are tolerant of adverse environmental conditions. Burrowing mayfly nymphs (e.g., Hexagenia spp., Ephemera spp.) are among the organisms most sensitive to adverse changes in the environment. Common in eastern United States waters, these are impressive insects. The large ivory, mottled with brown, animals carry massive mandibular tusks and have powerful forelegs adapted to aid in digging their U-shaped burrows in sediments. They live in their tunnels for up to 3 or 4 years, undulating their abdomens to pump food-bearing water through the tunnel and to pass oxygen-laden water over an extensive assemblage of filamentous biramous gills. Soil texture and composition are important because they determine the soil's cohesiveness or ability to retain the roof of a relatively large tunnel. Hexagenia were once common in Lake Erie. Their disappearance in midcentury has been attributed to pollution-induced limnological changes. In open waters of western Lake Erie in 1961, Hexagenia averaged <2 per square meter, compared to an average of 394 per square meter in 1930 (Carr and Hiltunen 1965). Considering that mature larvae weigh about 0.05 grams each, this was a tremendous change in the fish food potential, of this insect type, occurring in the lake. Burrowing mayflies remain important in many lakes and rivers of the Upper Midwest and Northeast. Their large size and abundance make them important fish foods and desirable as fish bait. The harvesting of nymphs from some waters contributes to the fish bait industry and has been extensive enough to require regulation in Michigan (Hunt 1953).

Leeches are sediment dwellers. Most species are small scavengers or prey on other invertebrates. Some are parasitic on fish and other aquatic organisms, a few on warm-blooded animals and man. Large Haemopis may extend to a length of 18 inches when swimming (Pennak 1952). Most leech species are small. Those species large enough to bait hooks can be found with fishermen and bait dealers.

The value of soil-dwelling invertebrates as fish food is underrated in America. One reason for this underrating is that we place low value on the fish species that consume these invertebrates: carp (Cyprinus carpio), suckers (Catostomus and Moxostoma spp.), and catfish (Ictalurus spp.). In the opinion of many, these fish only muddy the water and compete with more preferred species for space.

Many of our sport and fine-food fish have relatively low percentages of sediment-dwelling organisms reported in their diets, based on stomach analyses. These data are also usually qualified as from adult or harvestable-size fish. Many texts used to train professional fisheries workers discuss fish foods only in a generic sense. Little is known about the food habits of larval and juvenile fish, but this may be partially because we are still learning how to identify the early life stages of many important game and food fish. We do know that most young-of-the-year fish are found in habitats different than adults. In rivers, the quiescent pools and backwaters are the nursery areas. Here, the young do not have to cope with strong currents, and benthic conditions favor the burrowing forms of invertebrate fish foods. Adults of many of the more valued fish species rely heavily on large organisms, such as minnows, large insect larvae, crayfish, and even avian and mammalian animals, for their food, a matter of forage efficiency. Minnows or forage fish add a step in the food chain, but the life history and food habits are not known for many that are the basic food supply for game and food fish of human interest. The very young of even the most piscivorous species of fish are nourished by much smaller organisms that they can efficiently catch and handle. There is an abundance of the sediment-dwelling invertebrates available to them where they live.

Soviet scientists may have greater appreciation of the sediment-dwelling benthos than do Western scientists. Many of these benthos lack chitinized body parts (worms, leeches) or have only a small portion of the integument chitinized (Diptera larvae head capsules). The digestive processes of fish are rapid on these soft bodied animals, and within a very short time (30 to 45 minutes) the remains in the alimentary canal are not readily identifiable. Setae from worms can be observed, but much higher magnification than ordinarily used in stomach content analyses is required. Even when setae are observed under high magnification, we only have a note as to presence of worms in the diet, since there is no way to correlate setae numbers with numbers of worms or mass (Grigyalis 1972). The integument of worms is somewhat resistant to digestive destruction and will pass through a fish, but these empty skin sacks are nearly invisible and are difficult to find, even when specifically searched for and when their visibility is enhanced through the use of biological stains (Galinskii and Nikitin 1972). Chekanavoskaya (1981) notes that fish tend to graze or bite off the posterior end of oligochaetes sticking out of the burrow and up into the water column. The worm then regenerates the missing posterior portion. Frequent occurrence of worms in museum collections missing posterior segments or with regenerated ones was attributed to the "nibbling" of fish on the exposed parts of the animal. In summary, the Soviets, using special techniques, attribute much greater fish food value to the sediment-dwelling invertebrates than we have. Generally, we Americans give them a minor, and probably inadequate, role in the natural fish food resource overview.

Predators

Invertebrates that consume other invertebrates may be found everywhere. When visualizing a predator we usually think of a robust, agile, swift, and well-toothed animal that stalks, pursues, or ambushes weaker smaller animals. The megalopterans, hellgrammites or larval dobsonflies (Corydalus) and alderfly or fishfly larvae (Sialis), meet all of the typical criteria for a predator. The long-lived (2 to 5 or more years) larvae are among the largest (can grow to >3 inches long) of aquatic invertebrates. They are equipped with formidable pincher-like mandibles and can capture, kill, and devour most other members of the benthic community.

In direct contrast to the megalopterans, we find a number of invertebrates that are very subtle predators. Parasites are "cousins" of predators, chronic instead of acute consumers of their prey. The benthic forms are so secretive that we rarely encounter them. Hymenoptera are rarely aquatic species, but some are internal egg parasites, and a few species are minute ectoparasites on caddisfly pupa. Dipteran parasites are more common, but still scarcely encountered. Many of the marsh flies (Sciomyzidae) are larval parasites of snails. The parasites of fish food organisms are not fish food unless they inadvertently become so when their host is consumed.

Every order of insects that lives in aquatic habitats has predatory species, or at least omnivorous ones. None is known to specialize in specific prey species. They may appear to select certain prey, but this is probably the result of both predator and prey living in the same habitat. They probably will attack and consume any other animal they can cope with. The best examples of carnivorous aquatic insects are the Odonata (dragonflies and damselflies), where all nymphs are aggressive seekers of other aquatic animals, including small fish and tadpoles. Their bulky morphology limits many species to slow or quiet waters. Most lie in ambush or stalk their food, but there are several species that can be found prowling the interstitial spaces of rubble in riffles.

Many aquatic beetles (Coleoptera) and bugs (Hemiptera) also exhibit carnivorous food habits. Their food is not limited to fellow invertebrates, and they are a common problem in fish hatcheries, where substantial quantities of juvenile fish succumb to these strong aggressive swimmers. In these orders, especially the Hemiptera, many examples of the piercing feeding mode can be found. The mouthparts are modified into a piercing hypodermic needle used to suck body fluids from prey held in powerful forelegs. The nearly intact prey carcass is abandoned to aquatic scavengers.

There are a few species of carnivorous caddisflies (Tricoptera). Most mayflies (Ephemeroptera) are herbivores, but carnivorous species occur among some of the less common genera. Diptera is a large order with many species that are carnivores. Diversity in form, habitat, etc., is carried over into feeding habits, and carnivorous species are known from about half the families common in rivers. The Plecoptera or stoneflies are active nymphs that appear to be potential predators, but the order is probably evenly divided (in numbers of species) between herbivores and carnivores, with the latter most frequently represented in the families Perlidae, Perlodidae, and Chloroperlidae.

Carnivorous or predatory invertebrates add complexity to the usual simple food chain or food pyramid concepts of production-oriented ecologists. Benthos are generally referred to as secondary production, based on their consumption of plant life. Fish, which consume the invertebrates, are the tertiary production level. Carnivorous invertebrates add another level of production in the scheme. Carnivorous invertebrates are in direct competition with fish for the same herbivorous benthic animals. Though these invertebrates are also fish food, they add another step in the food chain production to the final consumer, man. An amino acid molecule ingested by man consuming a fish may have been through its role as protein in four, five, or more organisms instead of the usually thought of three. In addition to the direct competition between invertebrates and fish for the herbivorous prey, we find additional efficiency losses in food conversion. These losses are frequently estimated as about 90% for each consumer level. Long food chains are inefficient, with high risk of supply loss to the end link consumers. Some theoretical ecologists thought predaceous fish food organisms would appear to be competitors with fish, wasters of food, and at best an inefficient luxury link in the food chain. For maximum production efficiency of fish should we manage waters to minimize the quantity of predaceous unused invertebrates? In practice, the carnivorous invertebrates increase the efficiency of fish production. They have preyed on minute organisms, collecting them into larger organisms that then can serve as efficient food particles for fish. A large dragonfly may represent the assemblage of several times its biomass in microinvertebrates that individually would not be worth the energy to hunt and pursue by the much larger fish. Without the large predator, many of the minute herbivores might not have their production made available to the fish. Studies on food to fish conversion efficiency show midge larvae to be excellent food when delivered, but if they must be hunted in a river, a fish may do better by eating one dragonfly nymph, which represents 100 midge larvae.

LIFE CYCLES, STANDING CROP, AND PRODUCTION

A significant problem in the study of fish food organisms and their production is how their life cycles affect the field data related to standing crop and production. I will not go into the details of organisms' life cycles; however, I will touch briefly on some of the life cycle characteristics that must be factored into an understanding of fish food dynamics. The practicing biologist must become familiar with the various life cycles to gain a better comprehension of the fish food resources and the community assemblage being dealt with. Familarization is about all benthic biologists will be able to undertake, and they will soon find that there are wide variations in life-spans and growth patterns of even closely related species. There is a wide horizon of opportunities for the life cycle study of many species where nothing or at most very little is known. Until more specific knowledge is available, we must assume that for unstudied species, the life cycle is similar to a related species on which information is available.

Life spans of aquatic insects vary from a couple of weeks to a few years. Those species with short life spans may have several generations or broods in a single year. Their numbers or biomass present at any one time may be small, but the annual production is the sum of the individual generations or broods grown in a year. In contrast, a long-lived species' annual production is divided by the number of years in its life span to allocate production to a per annum basis. Production by species with highly varied life spans may or may not be similar. Data from an instantaneous sampling of the population may be misleading unless adjustment or compensation is made during data interpretation. This does not imply that single or occasional sampling data of the standing crop is not valid. Most of the aquatic insect species have but a single generation per year. The minority or atypical species may balance each other out. Relatively scarce multiple-brood species could equal the more abundant long-lived species in annual production. The data are also going to be compared on a relative basis to some other time, place, or stream, where the same life cycle effects are taking place. Data are meaningless in themselves and only have meaning when related to other similar data. With long-lived species, it is possible to find distinct size-classes of nymphs or larvae in the sample, each representing a different brood or year-class. Insects are not the only benthos that have different life spans and broods. Some species of Oligochaetae take several years to reach sexual maturity; others may mature and reproduce within weeks of hatching. Obviously, those invertebrates with short life spans and high breeding potential can more rapidly respond with population increases to favorable environmental conditions.

Pupation and adult emergence to terrestrial life cycle stages can also affect the data for benthic organisms. Many pupa and all adults of the mayflies, stoneflies, true flies, caddisflies, dragonflies, damselflies, dobsonflies, and fishflies are terrestrial. During the adult phase, these species may not be present in samples of the benthos; this is particularly true for single brood and mass emergence species, when the entire population is airborne adults. An adult phase may last for a couple days to several weeks. Benthos samples taken during or shortly after this time period may lack specimens of a species normally quite abundant. With other species, there may be a rather steady and continuous period of emergence throughout a prolonged season, with favorable weather.

Several species appear to inhabit a waterway for only a few weeks each year, but this is a product of sampling anomalies. Some species remain in a dormant egg stage through much of their life cycle. Other species remain in a semidormant or prolonged early instar stage. The minuteness of their size makes them inapparent without special sampling efforts; they pass through a standard number 30 sieve. A first thought is to expand the sampling effort to include the eggs and early instar specimens. Use of finer screens and optical aids might find these stages, but the information gained would be at great cost. When environmental conditions, time, or other factors become right, within a few weeks these usually dormant animals will hatch and grow rapidly to complete the instars remaining in the larval or nymph portion of their life cycle. They then emerge as adults to again "disappear" from the waterway.

The high reproductive potential of insects enables them to respond with sudden population increases when environmental conditions become more favorable. For example, Barr Lake, near Denver, Colorado, is an irrigation reservoir that was filled each winter with municipal sewage, some partially treated, some untreated. The water quality was inadequate for habitation by macroinvertebrates throughout much of the year. Benthic samples taken in May lacked animals. In early summer, conditions became tolerable for the hatching and development of eggs and chironomid larvae. The new stocks originated from egg-laying, immigrating adults. The larvae thrived in the shoal waters, where oxygenation was maintained by wind and wave action. By August, large numbers of the chironomid larvae (bloodworms) were approaching maturity and starting to pupate (Figure 5). In September, adults were emerging in numbers large enough to create nuisance swarms of flies in the surrounding areas. The conditions of large quantities of food for the larvae and the lack of competing or predaceous aquatic life favored the population explosion.

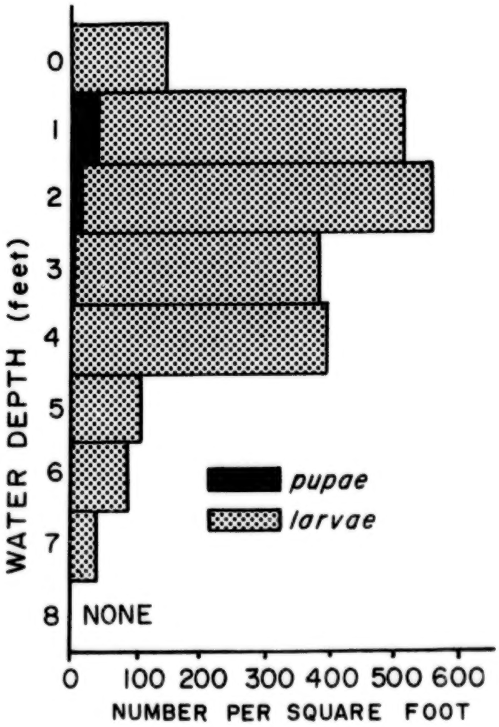

Figure 5. Distribution of midge larvae or bloodworms and their pupae in Barr Lake, Colorado, August 1964.

Season of the year will affect the quantity of animals and species found in benthic samples. Late winter stream samples will usually contain the following compared to other seasons:

(1) the largest biomass of organisms,
(2) the most species, and
(3) the lowest number of individuals per species.

These characteristics are the result of aquatic life cycles, growth of the insects, loss of individuals by attrition from competition and predation, and factors inherent in the sampling methods and technology. Figure 6 illustrates the seasonal fluctuations one can expect in benthic sample data.

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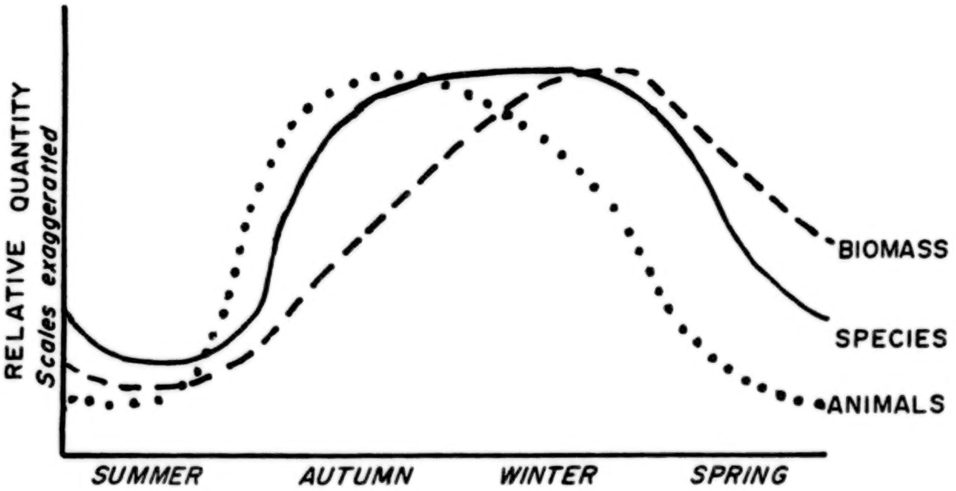

Figure 6. Seasonal changes in population characteristics data for benthic organisms.

The number of species found will be lowest in summer, when many insect species are in the terrestrial stage of their life cycle, and the eggs or early instars of the new generation are not yet present or detectable with the sampling procedures used. Many immature insects begin to reappear in the samples and the number of species increases as autumn progresses. For example, in the South Platte River, Colorado and Nebraska, samples taken in October had about 20% more genera than were found in August at the same sample sites. By winter, most insects have returned to the larval or nymph stage of the life cycle and have grown to samplable sizes. The number of species sampled remains relatively constant throughout the winter. Only a few species have winter terrestrial adult phases and breed at this season of the year, notable are some species of stoneflies (Plecoptera). Theoretically, there may be a slight increase in the number of species found as winter progresses and several species' dormant eggs hatch or very slow-growing immature specimens of some species are again found, but this change may not be detectable because of the variability of the sample data. Beginning in early spring and progressing into summer, adult emergence of the species results in a steady decrease of the variety of kinds found in the stream. In midsummer, the annual minimum diversity will occur, and then the annual cycle starts over as the immature stages reappear as benthic organisms.

The theoretical maximum number of individuals in the river would occur in late summer as the millions of eggs of all species are hatched. The maximum

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number will occur in the samples sometime in late autumn and early winter, when the larvae have grown sufficiently to be retained by the sampling equipment (Figure 6). Throughout the winter, there is a steady decline in the number of individuals as mortality occurs from inter- and intraspecific competition and predation. A rapid decline in the total number of benthic organisms begins with the water warming in spring and an increased rate of adult emergence.

Biomass of fish food organisms will be the lowest in warm or summer seasons (Figure 6). Again, a major factor is the absence of many species that are in the terrestrial adult phase of their life cycles. Another factor contributing to the decrease in biomass is a rise in predation by both fish and predatory invertebrates, whose metabolism and feeding activities increase as the water warms. Cooling autumnal waters are accompanied by reduced predation, immature nymphs and larvae of many species reappearing in the waterway, and the growth of millions of progeny. There is a very low survival rate of the benthos; less than a hundreth of a percent survive from generation to generation. The steady biomass attrition from the mortality of individuals caused by numerous factors is at least off-set by the steady growth of the surviving specimens. The surviving individuals will collectively have the greatest biomass in late winter.

The integrated products of specimen numbers, number of species, and biomass illustrated in Figure 6 show that the most fish food occurs in a river during winter for all three usually measured population parameters. All three measurements would have their lowest values in summer; however, the vast majority of standing crop data on fish food is from the summer season. Not only is the human working climate better, but the population of fisheries scientists is supplemented by graduate students and their professors. Summer fish food data are for the minimal standing crop of organisms. As of now, the percent of the maximum standing crop that this summer data represents is unknown. These summer data, however, are adequate to draw conclusions from. If there is sufficient fish food to meet the demand during the summer, a most active feeding and growth period for the cold-blooded fish, there should be a surplus during the colder seasons when the species, individuals, and biomass of the macroinvertebrates is greatest, and fish feed less or not at all.

DRIFT

Periodically, many fish food organisms are detached from the stream bottom and are found drifting downstream, temporarily suspended by the currents. During this short time of planktonic behavior, they constitute what we call drift. The time spent drifting is only a small portion of the total life span, but for some species it appears part of their routine to be detached from the benthic habitat. While drifting they are much more vulnerable to predatory fish. Swimming, prowling, or sprawling insects and crustaceans are the principal components of the drift. Simply by letting go of the substrate, they are swept away for a short time and distance before they sink to the substrate or make an active effort to swim back down to it. Species that are usually strongly attached, such as the sucker-equipped black fly larvae (Simulium spp.), are also frequently found in the water column for short times and distances, sometimes remaining attached to the place of origin by a silken thread before reattaching at a new downstream site. Case-building larval forms, such as the caddisfly larvae (Trichoptera), are also found in the drift when they intentionally or inadvertently detach. Burrowing life forms are less common in the drift, apparently remaining in their protected tunnels and burrows except when increasing stream velocities scour them into suspension.

Emerging insects are suspended in the water when nymphs or pupae are migrating from the bottom to the surface and undergoing ecdysis to the adult life stage. When large numbers of a species are undergoing this emergence, fishermen refer to it as a hatch. Fish feeding activity increases at such times, often with an absence of caution. The hatch-related drift is a one time activity in the life cycle and should not be confused with the periodic drift phenomenon.

KINDS OF DRIFT

Waters (1972) recognizes three basic drift types as well as varying degrees of interaction between them.

1. Catastrophic drift. This usually results from physical disturbance of the bottom, which dislodges benthos. Typically, it is associated with flood flows and velocities that scour and loosen the bottom substrates. Organisms are swept away or must abandon the unstable substrate. Coarse gravels and rubble when moving are dangerous to the inhabitants because they act as a "ball mill," grinding and crushing the animals and plants. Other adverse environmental effects, such as drought, high temperature, anchor ice, and pollutants, may induce abandonment of the habitat and are factors stimulating or inducing catastrophic drift.

2. Continuous or constant drift. There appears to be steady flow of low but relatively constant numbers of benthos detached from the bottom and temporarily suspended in the water column. This might be explained as a product of accidents. In normal activities, there is a probability of lost footing by an organism, which is then swept downstream for a time before it settles or swims back to the bottom.

3. Behavioral drift. This involves large numbers of a species' population and occurs in rhythmic patterns. A diel, or 24-hour day-night pattern, has been observed for a number of species in many parts of the world. Most studied are the mayflies (Baetis spp.) and the crustacean Gammarus spp., where the number of drifting animals sharply increases at dusk, continues relatively high through the night, and declines again at daybreak. Theoretically, these forms may be more active at night, foraging when the risk from sight-feeding predators would be reduced. Their night activity increases the probability of accidental input to the drift. This theory doesn't hold, however, if the caddisflies (Trichoptera) are considered, because many of these are day-active in their drift behavior. Various drift intensity patterns have been observed, but light intensity appears to be the dominant regulatory mechanism. Some periodicity has been observed in some species maintained in continuous dark or light, indicating there is some inherent biorhythm or "clock" within the animals. Some day-predominant drift species could be temperature-induced to drift; solar warming of the water may make these species more active and thus more susceptible to drift. There may be other rhythmic behavioral patterns based on time or even lunar cycles, but the strong day-night diel cycles mask other periodicities.

Needham (1928), studying terrestrial insect input by measuring their "drift" in the water, also noted and reported large numbers of benthos drifting. Observations continued sporadically until after World War II, when interest in drift phenomena increased, and several specialized studies and investigators appeared on the scene.

The European school of thought was based on ethnology. Continued drift downstream should tend to depopulate the upstream reaches of a waterway, and there must be instinctive compensatory responses within a species to account for maintenance and repopulation of the upstream river reaches. Without compensation for the loss to drift the benthic populations eventually would be eliminated by drift loss. Species' larvae or nymphs should show strong rheotaxis or upstream migration instincts to offset their downstream drift. Some species have adults that tend to migrate upstream prior to ovipositing or egg-laying and thus offset the downstream drift during the larval and nymphal stages of the immature aquatic life forms.

The American school of thought was based primarily on population dynamics and surplus production. The reproductive potential of a species is much greater than necessary to maintain the species. As the surplus immature specimens grow they overpopulate an area and compete for the necessary life essentials of food and space. The process of competition forces the surplus immature specimens into poorer niches where the probability of dislodgment increases or migration becomes necessary. This could explain the constant drift. Diel or behavioral drift in day or night peak periods is dependent upon whether the species are day- or night-active. Enough immature specimens would persist in the area to ensure species reproduction, and the drift phenomenon is a migration of surplus nymphs and larvae through a continuum of downstream translocations of excess individuals.

The European school incorporates the idea that there is a genetic component to drift, which explains why some species are drift prone while others are rarely found in the drift. All species should be subject to over-population pressures and dislocation potentials. All species tend to maintain relatively steady long-term population levels, including the drift prone species, indicating there should be some upstream movement to compensate for the downstream movement. Studies designed to show upstream movement have shown no gross movement of the benthos upstream. Scuds (Gammarus spp.) are drift prone animals, and there is no airborne adult phase to transport eggs upstream for restocking of the headwaters. Studies are both pro and con for support of a strong rheotaxis response by Gammarus.

Drift prone species are those with large numbers in the stream, short life spans, high reproductive potential, and rapid growth. They may also exhibit egg diapause or early instar aestivation, and they live in niches such as the upper surfaces of rocks and the fronds of vegetation that are most exposed to the currents. A slight footing error, relaxing of an attachment sucker, or weak attachment of a case dwelling would increase the risk of entering the drift. Of the case-building caddis larvae, Brachycentrus spp., are probably the most commonly reported in the drift. Brachycentrus builds a square or chimney-shaped case of organic detritus particles and weakly attaches it at the front edge to the top of a stone or other substrate, with the long axis of the case trailing in full exposure to the current. The weakly attached case is not streamlined and has no or very little ballast, because the materials have a specific gravity of essentially 1.0. The case can be seen harmonically vibrating in swift currents. No other caddis selects such a precarious position and uses such apparently poor engineering, materials, and anchoring system; but it works. Other current-exposed caddis species (e.g., Hydropsyche, Cheumatopsyche, Molanna) live in extensively anchored silk nets or streamlined rock-ballasted cases that are well anchored with secreted cements. Most caddis species that use low specific gravity building materials, have poor or no streamlininq, or are free-living forms with instincts to inhabit quiescent waters or use the shelter of interstitial spaces within the substrates.

For those interested in the detailed study of drift, the works and review articles of Waters (1965, 1969, 1972) are strongly recommended.

DATA EXPRESSION

In the study of drift, two data expressions are frequently encountered:

(1) density units of some configuration, e.g., animals per cubic foot or cubic meter of water, and

(2) rate units, which incorporate flow and time, e.g., animals per meter second, or animals per hour or day related to cross section or the total stream flow.

The velocity of the water mass determines the rate or quantity of transport. Water with the same density units of animals, when doubled in velocity, transports twice the animals per unit of time, because twice the water passes a point per unit of time. Thus, density units cannot be compared unless the water velocities are identical. Further discrepancies occur between density units when the cross sections between points compared vary.

A complicating problem in the analysis or comparison of drift is the cross-section of the stream in relation to the wetted perimeter of the stream. Drift studies usually do not consider this ratio or the changes that may occur if the ratio changes. The wetted perimeter is the space available for benthic production. If the stage of a river rises to effect a doubling of the mean depth there would not be a significant difference in benthic space, but the volume of overlying water in which the drift organisms would disperse would be at least doubled. Thus, we would expect unit densities to decrease to about half with a doubling of the stage, with the assumption that the emigration rate from the substrate to the water column does not change. But, with an increase of stage or cross-section there is a substantial increase in current velocities because of a reduction of drag or friction for the average water particle in contact with the atmosphere and bottom. Laminar flow increases and turbulent flow decreases. Assuming velocity does not also effect an increase in emigration rate from the substrate through dislodgment or other factors, what appears to be a numerical decline in unit density could actually be an increased drift rate because of the velocity (units per time) passing through a cross-section. Likewise, a drop in stage may produce more organisms per unit of water; but without compensation for flow, quantitative drift rates do not exist, i.e., the data are qualitative only. Velocity increases should mechanically increase the benthos emigration rate, especially those velocities that would institute instability or scouring of the substrate. Animals have been found drifting at a rate of 14,900,000 per square meter cross-section per day. With numbers of this magnitude it would appear that in a very short time a stream would void itself of the species involved; but it doesn't.

POPULATION AND DRIFT DYNAMICS

The following are some aspects of drift phenomena.

1. Biologists accept the fact that drift is a mechanism that increases the availability of benthic foods to the fish. It is a natural delivery system that carries food to fish at their feeding stations. This system is much more energy efficient than for the fish to swim against strong currents while foraging. A suspended invertebrate is surely more visible than one on the substrate, thus giving advantage to sight-feeding fish. Visual feeding is the habit of most of our food and sport fish. Though trout and other game fish will occasionally actively root in the substrate, their preferred feeding

style is to snatch a drifting food item. The forage fish, e.g., minnows (Cyprinidae), darters (Etheostominae), suckers (Catostomidae), sculpins (Cottidae), are much more apt to be benthic feeders, or even live in and on the substrate, than are the higher trophic level fish that man is most interested in.

2. Drift serves to transport fish food organisms from inaccessible sites to the fish. Shallow, swift, and turbulent riffles are not often used by pool-dwelling fish. Invertebrates drifting from the riffles supplement the food supply in the fish-inhabited pools. This makes the entire stream a food production area, rather than just those portions physically occupied by the fish. Without drift, the fish populations in pools could be more food-limited than space limited.

3. Drift provides an escape or relief mechanism from overcrowding. Surplus production is spread from site of origin, permitting remaining individuals to survive with the site's available resources. Because of rapid population growth of the highly productive prey species, the slower reproducing and growing fish population or predators are not able to respond with their numbers to use the supply of food prey. Emigration releases intraspecific competitive pressures at the foci of the population and ensures species survival with good well-being of the remaining individuals. Emigration or dispersal is an overpopulation relief mechanism for many vertebrate species (e.g., rodents, some birds, and even humans) and for some invertebrate forms (e.g., bees, locusts, and butterflies). It also applies to aquatic invertebrates that must disperse from the egg clutch or nursery area. In streams, random dispersal becomes downstream dispersal because of the currents. Upstream dispersal occurs, but it is a relatively slow process of crawling through and over the substrate; the distance gained can be rapidly lost if the animal is caught in the drift mode (an example of one step forward and ten backward). Quite obviously lateral dispersal is limited to the stream banks. Though dispersal occurs with all the benthos, it would be most obvious with these species exhibiting high reproduction potential, rapid turnover of individuals within the population, or a high production rate (especially in relation to standing crop, e.g. production/biomass (P/B) ratio).

Evidence to support a hypothesis that drift is related to population density and thus tied to competition has been found in several studies. Hildebrand (1974) found that high percentages of animals drifting was a function of their food supply. Proportionally less animals drifted when their food was abundant. He postulated that drift was a product of the probability of dislodgment during the process of foraging for food; lower food densities required more foraging effort and thus a greater risk of dislodgement and drift. Dimond (1967) studied Maine streams that had been sprayed with DDT insecticide. The DDT pauperized the benthic fauna. Benthos populations returned to "normal" after 1-2 years. During this recovery period, drift rates and densities were very low compared to the numbers of animals on the substrate and what would be expected from the normal populations. This indicated that there were adequate resources and little or no competition between the members of a still growing benthos. A year or two after the substrate populations had returned to "normal" densities for these streams, the drift quantities began to increase. This appeared to be population density related. Apparently, the community viability had increased to the point that surplus animals were being produced. Although the earlier standing crop numbers appeared normal, more time was needed to supersaturate the benthos sufficiently to support typical drift densities. Walton (1978) tested the return of drift animals to the benthic habitat. Sterile habitats were occupied as readily as those with food, but the occupancy was only temporary, and the animals soon left to the drift state. The return was much more rapid in areas where food was available, indicating an abandonment of the less habitable areas. Dead animals in the substrate rarely returned to the drift, indicating that drift is not solely a physical or mechanical action of the currents, but is at least partially a product of the behavior of the living organism. Addition of predatory invertebrates to the substrate did not increase the drift rates of the herbivorous animals. Thus, the implications of interspecific competition, even the pressure of a predatory consumer, are quite low. The role of competition must be between individuals of the same species requiring the same niches.

New stream channels, those with physically disturbed bottoms (e.g., from flood scouring and construction activities), and those where the benthos was denuded by pollutants are found to be rapidly recolonized. Drift from populated upstream waters is the primary mechanism of recolonization. Leonard (1942) found rapid colonization of a new manmade stream channel for a section of Hunt Creek, Michigan. Within 1 week after flooding the channel, black fly larvae (Simulium) were occupying the substrate. Other data related to the rapidity of colonization are shown in Table 9.

Table 9. Colonization by invertebrate organisms in a man-made channel, Hunt Creek, Michigan (Leonard 1942).

Date	Number of species	Number of animals/ft^2	Volume of animals cm^3/ft^2
October 16 (channel flooded)			
December 20	8	187	0.2
January 24	19	701	0.9
January 27	19	999	1.3
February 4	21	1535	1.6

The winter season precluded reproduction from aerial insects as the mode of colonization. Thus, colonization had to be primarily from drift. Waters (1964) undertook a study to determine the recolonization of areas depleted of benthos by sampling the populations. He concluded that within 10 days the habitat was reoccupied at normal densities of mayflies (Baetis) and scuds (Gammarus).

How much drift should a stream have? Little or no drift would indicate that the stream's benthic populations are not up to carrying capacity. There is adequate space, food, and other resources for the animals, hence they have not begun to compete for needs that result in the surplus product being "pushed" from the benthic habitat. The carrying capacity may not be reached in some streams where periodic catastrophic drift creates strong cropping of the population. Catastrophic drift could be caused by periodic influxes of pollutants or flash flooding. The large quantities of fish food put into the water column by catastrophic drift may not be usable to the fish in the short time span available.

After a catastrophic drift, there may not be normal drift quantities until the population increases to occupy all the niches and surplus animals again occur to contribute to behavioral drift. During this recovery period, continuous drift would occur, but at a low level.

The individuals involved in classical drift will consist of all instars of the immature organisms. There is a tendency for the later instars to be more frequent drifters, probably because of increased competition as the organism and its cohorts grow.

In addition to light, temperature seems to affect the quantity of drift. More drift will usually be found at the warmer water temperatures of the summer season. This is a function of cold-blooded animals being more active during these periods. The result is an increased availability of the benthic production at the same time the cold-blooded fish predators are also most active.

Drift, as a function of production, should reflect a stream's capacity to produce fish food. Low quantities of drift should indicate that plenty of resources for the fish food organisms remain available for further expansion of populations, i.e., populations are not up to carrying capacity. Atypically low drift rates should indicate that standing crop is not at stream capacity, with little or no surplus production for the fish. Conversely, a high drift rate, excluding catastrophic events, should indicate a rapid production rate, populations at carrying capacity, and the availability of surplus production.

Drift is the product of the upstream loss of animals. Immediately after being swept away from the substrate an animal struggles to orient itself and return to the bottom. A strong swimming animal may return within a short time. Animals without swimming ability, such as elmid beetle larvae, mollusks, and worms, have to rely on the chance of currents carrying them back to the bottom, or on entering a reach of weaker currents where they can settle out of the water column. The time spent drifting is a product of the animal's swimming ability and the chance of turbulent currents returning the animal to contact with the bottom. The time suspended and the velocity of the currents determine the distance traveled per drift episode. Animals travel as drift in a saltatory fashion, but most of the time (99%) they are in the benthos. Drifting is not to the individual's advantage. Theoretically, the weakest organism is forced from an area by its stronger neighbors. A number of situations may be present when an organism lands in a new substrate site. Adequate space and resources are available for the immigrant; limited space and resources are available, but the immigrant finds weaker individuals that can be displaced; or the individual finds the site unsuitable physically, i.e, it is at the bottom of the pecking order in the new community of individuals. An untenable situation will force another migration within a short time. An individual will not travel great distances, even dead ones are returned to the substrate within a short time and distance (Elliott 1971). The invasion of a newcomer does not mean immediate space competition and exiting of a resident. The community first tries to absorb the newcomer, and competitive adjustment takes time before one of the colony "slips" into drift status. It is a process similar to that seen when watching sand particles drift along the stream bed--there is a constant flow of grains, but not the same grains because the settling particles are constantly displacing and replacing static particles.

The drift density in the water flowing over an area in relation to the standing crop of the area may be usable as an index of (1) the relative production/biomass values of the stream, (2) the turnover rates of the benthos, or (3) the overall well-being of the fish food resource. The number of organisms drifting over a unit of bottom per unit of time is a function of the density of bottom organisms. Drift, being a surplus of production, should have usefulness in determining a stream's benthic fish food productivity, at least in a relative sense. Absolute production cannot be measured based on drift, because drift is the residue of production after various removal processes have occurred:

(1) predation by fish,
(2) predation by predatory benthos,
(3) death and decomposition or scavenger consumption,
(4) emergence of adult insects,
(5) exclusion of eggs and minute early instars not taken by the sampling protocol,
(6) production stored in the biomass of the standing crop of benthos that must be sustained to provide a continuum of the species, and
(7) energy and nutrition required for the metabolism of the organisms (an important aspect when studying the quantity of resources required to support the benthos).

All of these factors reduce the gross production of a species. After these reductions, the net production remaining is the total potential fish food.

Waters (1962) proposed the use of drift to estimate the production of Baetis vagans, a mayfly with strong propensity to drift, in Valley Creek, Minnesota. The assumption was made that the drifting Baetis were the surplus animals produced on the riffles of the stream. The algebraic expression of Waters' procedure is:

$$P = \Delta B + (D_o + D_i) \tag{2}$$

where P = production during the time span of measurements

ΔB = difference in benthos biomass

D_o = biomass of the drift off or out of the reach

D_i = biomass of the drift into the reach

Most benthic data are based on a unit area (i.e., square foot or meter) and then extrapolated to the area of the stream, whereas Waters' method considers a reach of stream as the production area for the drift, which must then be reduced to unit area based on the total area of the measured reach. Waters measured drift into a riffle reach and out of the reach, the standing crop of bottom animals within the reach, and the change in drift quantities into and out of the pool at the foot of the riffle. He found production rates of 23.5 g/day in the riffle, or 0.28 g/m²/day. The consumption rates were 23 g/day, or 0.45 g/m/day (by implication the riffle area was 1.6 x the pool area). Presumably, brook trout, Salvelinus fontinalis, living in the pool were the principal consumers of the production in and from the riffle. A consumption rate of about 98% would be an unexpected rate of efficiency. Some of the specimens undoubtedly settled to become part of the pool benthos. Some Baetis may have been injured in the turbulent trip to the pool and subsequently perished, only to decompose or become food for scavengers; some were undoubtedly fed on by predators in the pool benthos, and some may have "walked" out of the pool back to an upstream or downstream riffle, which is their normal habitat. Conversely, some riffle production was probably consumed within the riffle by the few fish stationed there and by predatory invertebrates. Waters did not observe significant adult emergence during the time of the study, but this could be a loss factor when it occurs. Overall, the minor impacts of other factors involved in either the D_o or D_i data are probably insignificant or offset each other. The remarkable part of Waters' study is how close the production and consumption values match (23.5 and 23, respectively). The D_o and D_i values must be very close for a steady state population; if they diverge substantially, there is either a decline or an increase occurring in the population.

Waters' (1962) values are for one species during much of the month of July. Baetis and Gammarus are the predominant benthos in Valley Creek. These, plus minority fauna, and seasonal variation all affect the annual production of the benthos. Baetis may be a predominant animal in the July drift, but in other months other species may tend to drift more, especially in proportion to their numbers. Also, periodic catastrophic drift episodes, such as during spring runoff or spates, should not be discounted. These catastrophic episodes should pare the standing crop to below carrying capacity, and following the episodes there should be reduced drift until production has replaced the lost benthos and surplus above the carrying capacity is again generated and available to drift.

Drift should be a good indicator of the surplus benthic production that could be available to fish consumers with no effect on the continuity of the benthos species. Waters' (1962) approach can be modified:

$$P = \Delta B + (D_o + D_i) + E \qquad (3)$$

The addition of E was proposed by Hynes (1972) and represents the emerging adult insects, which are required to perpetuate the species, but are effectively lost to the terrestrial ecosystem. Emergence (E) would not be a factor for benthos that do not have a terrestrial adult phase, e.g., worms, leeches, crustaceans. For these noninsect benthos, ΔB must show some residual population for perpetuation of the species. ΔB for insects will probably also show some residual numbers, but, theoretically, the entire gene pool could be out of the river during the breeding season. The long-term, year-to-year ΔB must average zero if the populations are stable. Long-term ΔB changes would indicate ecological changes and shifts in species. A decline in one species may be offset by increases in one or more other species. A change in total biomass of all species would indicate a shift in the production rates for the entire benthic community. The gross production of benthos may underlie the shift in biomass, or there may be community shifts of species with different production or turnover rates. On a steady-state, year-to-year basis, emergence must remain relatively constant. Except for seasonal (and some animal) variability there can not be changes in the drift rates if a sustained yield of fish food is to be maintained.

The factor $(D_o + D_i)$ must be a positive number, more drift cannot be consumed in an area than is available. Thus, the magnitude of D_i would be an index of the fish food production, or at least the surplus after consumption. No matter how efficient the consumer community is, it is not capable of "gleaning" the last available food. The higher the D_i value (drift) is, the greater is the surplus of fish food above the demand level, capture capabilities, or needs of the fish population.

PRODUCTION AND DRIFT

The following factors affect the quantity of drift:

(1) the production of benthos,

(2) the consumption of the benthos and drift, which is a function of the consumer population. Few predatory fish in a stream could result in higher drift rates, when compared to other streams,

(3) the distance an organism remains in the drift. The drift is an aggregation of the benthic losses for some upstream reach of the waterway. Organisms persisting in the drift for great distances contribute to the aggregation for a longer time or a greater reach. The result is a higher density of animals accrued per unit of water; and

(4) the quantity of water the organisms are dispersed in. Doubling the flow rate will double the quantity of water in which the organisms are "diluted," thus the density of organisms will be halved.

Evidence leans heavily towards the hypothesis that drift is the surplus production. The organism species involved most in drift have short life spans and tend to have multiple generations in a year (bi-, tri-, multivoltinism). For most stream benthos, the annual biomass produced ranges from 4 to 5 times the average standing crop found, thus 70% to 80% of the production must be lost to natural causes or consumed, with predation by fish being the major factor. The most common drift organisms have atypically high production/biomass ratios (data from Waters 1977):

Mayfly, *Baetis*	8.4 - 9.7
Scud, *Gammarus*	6.7 - 6.2
Black fly larvae, Simuliidae	6.2 - 12.9

Organisms with low drift frequencies have atypically low production/biomass ratios:

Stoneflies, Plecoptera	2.3 - 3.8
Sowbug, *Asellus*	2.0 - 4.7
Crayfish, *Orconectes*	0.94 - 2.0
Snails and clams, Mollusca	0.14 - 3.5*

Effects of river discharge rate on the quantity of drift are not well known. Benthic production is related to bottom area. Discharge is a measurement of the volume of water passing over a relatively stable amount of bottom area, i.e., doubling the volume of water going through a channel would not appreciably change the amount of benthic space for production. There would be slight increases in the wetted perimeter, but the change would be only a small percentage increase. If the rise in discharge rate is only a temporary

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*Normally we would not expect mollusks in the drift because of habitat and their high specific gravity. If short life span and rapid turnover aid in high production/biomass ratios--the long life span contributes to a low production/biomass ratio. Exceptions to the general rule for mollusks are the pulmonate snail *Lymnaea* (*=Limnaea ?*) *peregera* (multivoltine, or several life cycles per year) and the limpet, *Ancylus fluvatilis*, (univoltine). These gastropods have respective P/B ratios of 11.5 and 3.3., extremely high for mollusks. European studies have shown *Lymnaea* and *Ancylus* to be fairly represented in the macroinvertebrate drift fauna (Elliott 1971; Armitage 1977). American studies have been in waters with fewer or no mollusks. *Ancylus* is not a North American genus, though *Ferresia* limpets, a close relative, are common in many streams, especially eastern America. *Lymnaea* species in America favor ponds and if found in streams are usually limited to quiescent back waters, frequently on the moist mud banks above the shoreline, and in these habitats would probably be subject to catastrophic drift only.

fluctuation, the newly wetted perimeter would not be involved in the production of benthos. At first flooding, the new portion of the bottom area does not have a standing crop, and a considerable length of time may be involved for invasion and occupancy of the "new benthic lands." Time required for benthos occupancy of vacant areas may range from 2 weeks to 2 years (Leonard 1942; Waters 1964; Dimond 1967). Drift prone animals have a rapid transport mechanism to facilitate colonization. Freshly inundated terrestrial grasses will be first occupied by mayfly nymphs (Ephemeroptera) and scuds (Gammarus), and it isn't until after lengthy periods of inundation that the slow-moving mollusks and worms make their way to these new habitats. The expansion of the wetted perimeter should provide more space for those organisms coming from animal-saturated areas. The result should be a reduction in drift. The relief, though, would be minor, because the permanent benthic areas would still have their invertebrate populations at or above carrying capacity. If there was a 10% increase in benthic habitat, a randomly drifting organism would only have a 10% chance of "touching down" in the new space; 90% of the drift would still return to occupied area. This minor population pressure relief should not make substantial changes in the drift densities or rate. With a 10% influx of drift into the new habitat, it would only take a week or two for the barren areas to be occupied at about the same density as the permanent habitat.

Figure 7 shows the much more rapid increase in volume of water compared to the square feet of stream bottom as the size of streams increase. The change would be less evident within a river than between different size rivers. A river has a very shallow U-shaped channel. Changes in stage, velocity, and discharge are normally all accommodated within this channel, and only the steep banks are wetted and dried. Most of the permanent benthos habitat is in the shallow bottom of the "U," which remains little changed in area except in extreme low flow conditions. Substantial increases in bottom area occur only when the river floods out of the channel and inundates the flood plain. This once in 2 years occurrence is temporary and is not usable for benthic production. In fact, it may be detrimental to benthos, because flows at this time may induce catastrophic drift, and the organisms involved can be lost after they are deposited and stranded when the water recedes.

This should not be interpreted to imply that flooding has an adverse effect on fish food or fish production. Some streams are subject to much more frequent flooding than the typical once in 2 years. Examples are southeastern United States coastal streams, and many streams in urban areas where man-altered watersheds have high runoff rates and are flash flood prone. Streams valleys with little rainfall infiltration have little groundwater input, and minimum stream flows are more frequent and severe. Frequent scouring of the stream beds and the erosion inputs of fine soils may be factors that limit the development of bottom fauna in many of these coastal plain streams. Southeastern coastal streams have very poor benthic standing crops, but fish populations may be outstanding. Many biologists feel that the fish receive much of their food as terrestrial animals inundated by the frequent floods during which the fish forage on the lands of the flood plains. Fish foraging on the flood plain return to the channel with the receding waters. Benthos do not develop in the short period of flooding of the riparian lands. Receding waters carry substantial quantities of organic materials from the riparian

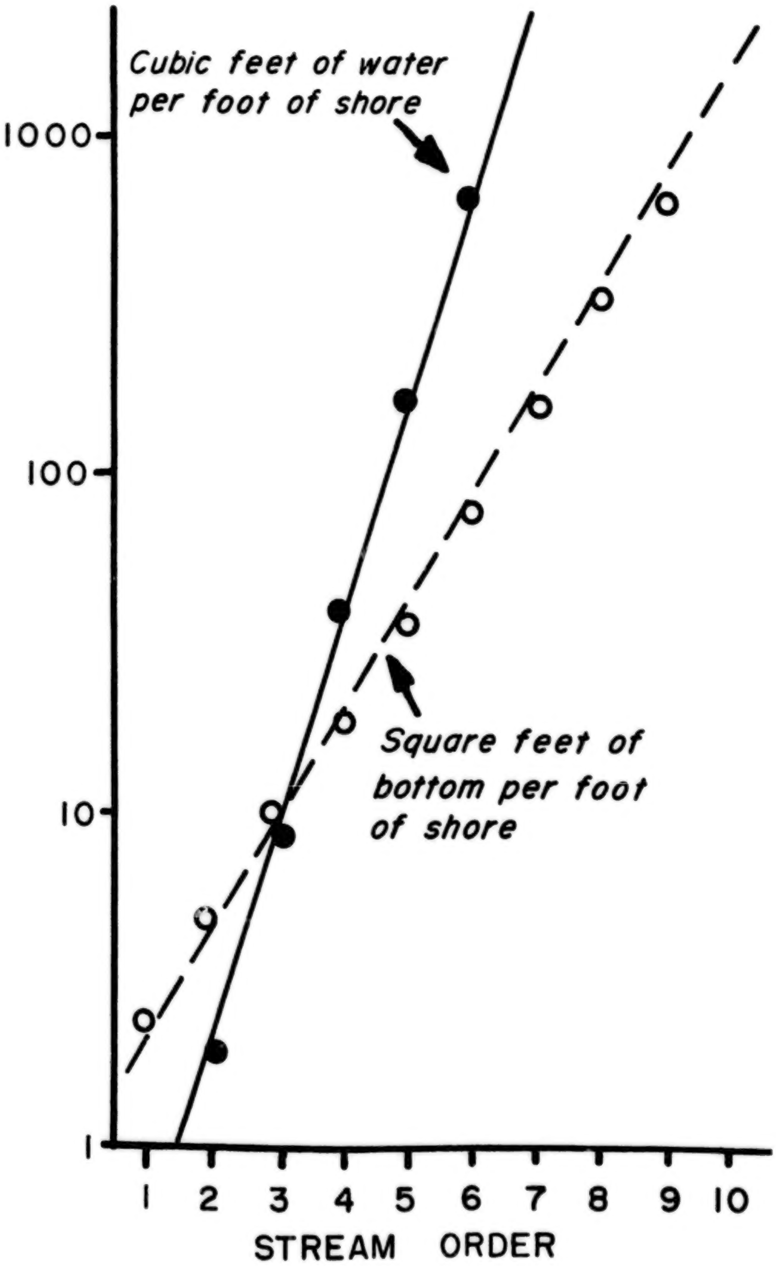

Figure 7. The relationship between the linear feet of shoreline and the volume of water and the square feet of stream bottom for various orders of streams and rivers. Note the steepness of the slope for quantity of living space for pelagic life versus the space for benthic life as streams increase in size (based on data from Keup 1985).

bottom lands back to the main channels of the black water streams that are colored from the organic leachates obtained from swamps and bottom lands.

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DISTANCE OF DRIFT EPISODES

The distance an organism will drift before returning to substrate has been the subject of several studies. Waters (1965) estimated that Baetis vagans (mayfly) and Gammarus pseudolimnaeus (scud) typically averaged a drift of 50 to 60 m. Elliott (1967a, b) estimated the drift distance for the aggregate of all invertebrates to average 10 m; McLay (1970) estimated that the average invertebrate drifts 10.7 m, with species differences ranging from 0.5 to 19.3 m. The difference between species is probably strongly related to the morphology and behavior of the animals. Heavy animals, such as limpets and stone-cased caddis larvae, drift only short distances. Animals with weak or no swimming ability, such as midge larvae (Chironomidae) and some mayflies (Ephemeroptera), are at the whims of the currents and appear to return to the substrate solely by chance or when velocity is reduced; their rates of return are the same for living or dead animals. Animals with strong swimming ability, such as some mayflies, leeches (Hirudinae), and scuds, have variable rates of return, depending on their reactions and behavior when in the drift mode (Elliott 1965). Black fly larvae (e.g., Simulium, Prosimulium) are a gourd-shaped "maggot" with little if any swimming ability, but they return quite rapidly to the bottom because they spin a silk thread that they attach to the substrate. If dislodged, they can follow the thread home. If the thread breaks, the trailing end will tend to become attached to some other substrate, and the larvae then reel themselves in to their new site. This safety-cord adaptation is probably a big factor in permitting Simuliidae to occupy the swiftest waters, including vertical walls at waterfalls and the spillways of dams. Edington (1965) noted that Hydropsyche larvae (caddisflies) tended to swim to the surface and then drifted at or in the surface film until they reached low velocity sites, where they then settled back to the bottom. Hydropsyche spp. and Cheumatopsyche spp., two rather similar caddisfly larvae in both morphology and habitat, have a small air bladder in the body cavity. Under stress they will inflate this bladder and increase their buoyancy. Both of these genera are usually well secured within an extensive silknet mass, and should not be prone to drifting except when forced from their secure shelters. Then, drifting would be an atypical act, the stress could induce bladder inflation, which would facilitate movement to the water surface during the drift mode. Transport at or in the surface film could be advantageous because of reduced visibility to predatory fish.

A number of efforts have been made to model the drift duration or distance traveled by a drifting animal (Waters 1965; McLay 1970; Elliott 1971; Keller 1975). The models are all species specific. They all have the characteristics of a typical exponential decay function:

$$N_x = N_o \ (1-10^{-Rx}) \qquad (4)$$

or

$$N_x = Ne^{-Rx} \qquad (5)$$

where N_o = original number of organisms in drift

N_x = number of organisms remaining in drift after passing a distance

R = a return coefficient based on the species physical and behavioral characteristics

x = distance

All studies show this relationship, which produces a smooth arithmetic curve or a straight-line semilogarithmic curve when numbers are plotted against distance. The slope of the curve is dependent on R, a coefficient for each species evaluated. The value of R is based on the species physical and behavioral characteristics or the ability to return to the substrate. A large R value produces a steep slope, which is indicative of a short drift distance and rapid return to the substrate, such as is found with actively swimming mayfly species. The literature contains numerous R values for the rate of return to the substrate. Unfortunately, these values are not comparable because they are based on distance and not time. Distance traveled is a function of the velocity of the water, which is a time function. Unless the water velocity is constant, coefficients for distance traveled are not comparable. They could be converted to time functions if authors had specified the velocity in feet or meters per second that the coefficients were determined for.

Elliott (1971) developed return coefficients for several benthic species, for several velocities, and for different seasons of the year. Elliott's return coefficients appear to be closely related to the velocity, i.e., a doubling of the velocity nearly doubles the distance traveled, or halves the coefficient value. This strongly indicates that the rate of return (R) or the distance traveled (1/R) is principally a function of time and the velocity of the water. Elliott expresses this as:

$$\frac{1}{R} = aV^b \tag{6}$$

where $\frac{1}{R}$ = distance traveled (average)

a = a constant for the species

V = velocity

b = coefficient for the species at the velocity

The return coefficients are all close to unity for the species examined. With such little variation, there is an implication that a sampling artifact exists. McLay (1970) also described exponential return of organisms to a stream bottom, but he always worked with the same water velocity.

It is quite likely, for all practical purposes, that the return coefficient does not exist. Elliott (1971) worked with velocities ranging from 10 cm/sec (0.33 ft/sec) to 60 cm/sec (1.96 ft/sec). To increase the velocity in a channel, the depth of the water must also be increased. Increasing the depth reduces the drag, Manning's constant, and increases the differences in surface elevation of the water in the reach, thus increasing the gradient or potential energy. Both the reduction in drag and the increase in water surface slope generate the increased velocities.

Distance traveled by a drift organism is not strictly the straight horizontal distance between two points bounding the upstream and downstream limits of the reach. The animal can and does move through the water column as it passes downstream. Waters (1965) studied the vertical distribution of drift within the water column and found that the animals were distributed throughout the depth range sampled. There was not a tendency for the distribution to be skewed with more animals remaining near the substrate; instead there was a tendency for a greater proportion of the animals captured to be taken near the surface. Waters could not distinguish if this was a product of greater density (animals/volume of water) or whether it was a result of a greater volume of water passing through the sample nets closer to the surface (higher velocity resulting from less effect of friction and turbulence induced by the irregular bottom). The distance or route traveled by a drift organism is probably a hyperbola. An insect leaves the benthic habitat and is carried upward and again downward as it travels the horizontal distance. The total distance traveled or the time involved in travel includes both the ascent and descent as additions to the horizontal movement. The vertical boundaries of its travel are fixed within the universe of stream bottom and surface (depth). Lateral movement could also be a factor, especially if a channel has large obstructions that produce meandering current. The change in depth associated with increased velocities could effectively increase the distance traveled and would be more apparent the shorter the horizontal distance in the reach studied. In a 10-m reach, increasing the depth from a half to a full meter would increase the distance traveled by the average animal one-half meter, assuming vertical travel was an equal probability, as is assumed in horizontal travel. This half meter increase in depth would add 5% to the distance traveled. Five percent is greater than the return coefficient variation from unity as derived by Elliott (1971).

Time is probably the primary factor for the drift period of an organism, and distance traveled is then a product of the velocity of the water and time. Each species reacts to being swept into the currents. The reaction varies from apparently none to active swimming to seek new substrate. Strong swimmers may actively swim upstream against weak currents. At very low velocities, 10 cm/sec (0.33 ft/sec) the return coefficients for some species artificially introduced to the currents are near or even exceed one. This means that some of the animals experimentally introduced to the water from the surface probably were capable of swimming upstream to a bottom site rather than drifting downstream to sites.

One might expect temperature to have an effect on the period of drift. The time in the drift mode should be a function of the activity of the animal; waters either colder or warmer than optimum should reduce an animal's capability of returning to the substrate. Elliott's (1971) work was performed in February (cold water), April, and June (warm water) in England, and the return coefficients did not follow a specific pattern or change significantly, indicating temperature had little effect on the drift distance. Elliott's (1967) data show that the frequency of drift (or density, animals per volume of water) increases during the more active and growing seasons for the species. Temperature may affect the possibility of the animal appearing in the drift, but if it has an effect on the duration of the drift period, it is minimal.

STREAM OR FISH PRODUCTION

From a fishery manager's viewpoint the quantity of drift should be a reflection of fish food resources, especially the fraction of production that would be available to nourish the fish populations. Most fish managers know little of the food resources on which they are basing fish management plans, policies, and other decisions. This is due, in part, to the inability to rapidly and economically obtain this information and to the difficulty of interpreting the data. Though research develops techniques and principles, it generally does not consider the application of the material to day-to-day operations. Meaningful application of new technology probably lags by several years its development.

Drift studies are an excellent example of research extending across decades of time with little use other than a contribution to the general knowledge of streams. Waters (1982) broke this trend and used drift to show fluctuations in benthic production followed by similar fluctuations in brook trout (Salvelinus fontinalis) populations. What fishery managers need is the ability to use drift density or drift rates as tools to ascertain if drift is contributing to the well-being of the fish stocks.

Drift as an estimate of the production of the benthic community has practical relevance (Muller 1959; Waters 1961). Standing crop at a point in time is strictly a measurement of the well-being of the stocks of fish food. Standing crop bears a minor role on the quantity of food organisms grown over a period of time. Much of the standing crop must be viewed similar to the seed stock of the farmer. Fish can consume from this standing crop, providing it is replaced in-kind by production within the standing crop. No fish manager could allow maintenance of fish stocks that would consume the breeding stocks without expecting depletion or shortages of fish food. Conversely, if there is an excess of food available, the manager could increase his stocks or production of fish.

Drift is fish food that can be consumed without risk of damage to the "seed" stocks. It also places the benthic yield of organisms in the water column, where it is in a more favorable position for the sight-feeding predatory fish. In the coarser riverine substrates, such as cobble and boulders, fish would be inefficient in extracting animal foods, especially those occupying the interstitial nooks, crannies, and crevices where much of the benthic space and cover occurs and detrital foods accumulate to sustain the benthos. This interstitial area includes the water-sediment interface and deeper zone called the hyporheic (Hynes 1972). Many microinvertebrates live here as well as the very young of the larger invertebrates. As the young macroinvertebrates grow, the hyporheic space becomes crowded and they are forced towards the water-substrate interface. The hyporheic zone adds to or expands the third dimension of the benthic area.

Schwoerbel (1961, 1964) studied the distribution of animals and their relationship to depth within the substrate and found as many as 34,000 animals per square meter of bottom when substrate depths to 10 cm were included. Usually, benthic samples are taken to a couple inches in depth and do not include this large a volume of habitat, nor do they include the multitude of micro animals not readily visible to the eye or collected with the sampling equipment. As a result, the numbers of macro animals reported are much lower. An excellent standing crop of macroinvertebrates sampled in the usual ways would contain animals at a density of about one-fiftieth of that found in Schwoerbel's more detailed study.

YIELD

The production/biomass (P/B) ratio should be a good indication of the excess food generated or potentially available to feed fish. With a P/B ratio of 4, 75% of the production (P) should be consumable without touching the biomass (B) or standing crop of benthos that serves as seed for the basis of production.

P - B = Surplus Food

Production - Standing Crop = Yield

Total - Seed = Net Consumable

Most drift investigations have dealt with selected species of animals that are prone to drift or at least have high densities and/or rates in the drift. These species have high turnover rates and production/biomass ratios and multiple generations or cohorts per year. There are also seasonal, or at least periodic, fluctuations in the drift as each cohort reaches periods of maximum growth or input to the drift. A species common in the summer drift may not even be noticed as part of the winter animal population because it may be in a resting stage, either egg or minute nymph or larvae. An animal abundant in early summer may be scarce or absent in August when the cohort has become terrestrial breeding adults. The number of generations or cohorts that develop in a year (voltinism) appears to influence the P/B ratios and the incidence of the animals in the drift. Waters (1977) summarized production and voltinism data reported in the literature (Table 10).

The problem with food analyses is that one cannot be species or cohort specific. Except for the large mollusks, the entire spectrum of macroinvertebrate animals can be viewed as potential fish food. Though feeding

Table 10. Production/biomass ratios of stream macroinvertebrates as summarized by Waters (1977).

	Production:biomass ratios	
	Range	Average
Multivoltine	3-16	8.3
Bivoltine	2-9	5.4
Univoltine	<1-9	4.5
Hemivoltine	<1-4	2.2
Mollusks	<1-5	1.7

studies show food preferences, they are probably a product of both availability and selection. Most animals, including fish, can and will shift their food preferences, if necessity dictates. If a fish can physically cope with a food, it will use it.

It would be impossible to undertake species by species investigations for all the kinds of invertebrates and then attempt to integrate the results. The benthic community is a product of the integration of all the environmental variables within the recent past. The standing crop reflects this integration of biological, chemical, and physical influences on the species composition and well-being. The drift should be the fish food yield or excess production of the benthic community, especially when there is minimal consumption by the fish. Waters (1977) concluded that the annual benthos production would exceed the standing crop by 6 to 8 times. He stressed that this value would not be a basic research tool, but that " . . . it would be useful in a variety of applications, such as resources management." The yield of fish food above the production to maintain the benthos should be:

$$P - B = F$$

$$\text{Production} - \text{Biomass} = \text{Food, yield, or surplus}$$

$$6 \text{ to } 8x - 1x = \text{Food}$$

$$5 \text{ to } 7x = \text{Food}$$

where x = biomass or standing crop on the substrates

Excess annual production moving as drift should be 5 to 7 times the standing crop found on the bottom. This would indicate a turnover equal to the standing crop every 50 to 70 days on an annual average. One would expect higher than average production during the warm water seasons and less than average during the cold water seasons. Using the 50 to 70 day turnover, one would expect between 1.5% to 2% growth of the benthic population per day, or generation of surplus animals contributed to the drift. A unit area of bottom should have 1.5% to 2% of the standing crop of benthos in the drift mode. This has been found to be a reasonable approximation (Waters 1965). Depth would influence the density of the animals in the water; doubling the depth would halve the density and halving the depth would double the density. Velocity should not affect the density, but it certainly is a factor in the rate at which organisms are transported over an area or in the number captured in a net. The total catch per unit of time must be divided by the quantity of water passing through the net, which is a function of velocity. A net with a square-foot opening exposed to a velocity of 1 foot per second would capture the organisms from 3,600 ft^3 of water in an hour. The quantity of organisms would need to be divided by 3,600 to determine the density of animals per cubic foot of water. This density multiplied by the depth of the water (vertical dilution) should approximate 1.5% to 2% of the benthic standing crop for waters of typical production. Water with fewer water column animals expressed as a percentage of standing crop would be atypically low in production; conversely, depth adjusted high drift densities would indicate that the water is more productive than typical. Some waters may have a high standing crop with low production, or vice-versa. For example, typically cold waters have high standing crops of animals but low production rates compared to warmer waters. Arctic waters have abundant numbers of long-lived slow-growing fish that will yield little long-term sustained fish catches or harvest, but initial harvest may be great because of accumulated standing crop. The same high relationships can be found for benthos. For example, Butler (1982) found Arctic chironomids with 7-year larval life spans, several-fold the length for most temperate species.

MEASURING DRIFT QUANTITY

The quantity of drift might appear to be a function of the distance traveled per drift episode of the individual animal. This is not the case, because the individual animals are moving in a continuous saltatory fashion involving all the animals. The individual animals move in short excursions, with a typical distance for the species and probably for instars within a species. The instant an animal returns to substrate there is an equal chance of another animal entering the drift mode.

The drift rate would be a function of the density of animals times the stream's discharge:

$$\frac{\text{animals}}{\text{volume}} \times \text{discharge} = \frac{\text{animals}}{\text{time}}$$

$$\text{discharge} = \frac{\text{volume}}{\text{time}}$$

This can produce astronomical numbers, but densities actually can be relatively low. For example, at densities of two animals per cubic foot of water moving at a velocity of one foot per second, a net with an opening of one-square foot would capture 172,800 animals on a daily basis, because a square foot ribbon of water about 16.4 miles long would pass through the net each 24-hour day. Densities actually tend to decrease as streams increase in size, and total numbers increase as the size, discharge, or wetted perimeter increase. Large rivers should have low densities of animals spread throughout the water column, slightly fewer animals in the total depth column, but higher total daily drift rates than a small stream. Though total numbers are large, they are diluted through much more water, which decreases the density.

The quantity of macroinvertebrates in natural streams should approximate 150 animals per square foot of coarse gravel or cobble riffle, and these should weigh about 1.5 grams total (1,500 animals weighing 15 grams per square meter). With 1.5% to 2% surplus production from this standing crop, there should be generated 2 or 3 animals or 0.02 and 0.03 grams of drifting fish food from each square foot of substrate per day (between 20 and 30 animals or 0.2 and 0.3 grams per square meter per day). Extrapolating these numbers to acres and hectares, the usual units of comparative production, we get 85,000 - 128,000 animals, weighing 0.85 - 1.28 kilograms, per acre, or 200,000 - 300,000 animals, weighing 2 - 3 kilograms, per hectare. A riffle 100 yards long and 10 yards wide would produce 54,000 - 81,000 drift animals, weighing 540 - 810 grams, each day. On an annual basis the drift would be on the order of 700 - 1,000 kilograms per hectare of benthos. This is sufficient to support the production of 70 - 100 kilograms/hectare (28 - 40 pounds per acre) of fish, with no supplemental input of terrestrial foods. This is within the productive range of the world's salmonid streams (Waters 1977).

Measured densities in N/volume must be adjusted by the mean depth of the water, since the animals are dispersed through the water column. Comparing this quantity to the quantity in the benthos we should typically find the 1.5% - 2% of substrate animals in the water column (drift):

$$\frac{D_m \times N_v}{B_a} = \text{Percent} \tag{7}$$

where D_m = mean depth of water

N_v = animals per volume of stream water

B_a = animals per area of stream bottom

Percent = percentage of benthic animals in the drift mode

Note: This equation will work with either numbers or biomass. Dimensional measurements are either English or metric, providing all are in one system. If the value for percent drift density is less than 1.5% to 2% of the bottom standing crop, then the production of the benthos is atypically low; if greater, production is atypically high.

Measurements must be made in the fish food production areas and where fish consumption is minimal, i.e., riffles. Drift samples must also be taken well downstream into the riffle production area to ensure that an equilibrium between the animals entering and returning from the drift mode is obtained. Typically, this should be at least 20 m, and preferably 50 m, especially in very swift water, downstream from the head of a riffle. These values are based on the drift distances for the more active benthic species (Waters 1965; McLay 1970; Elliott 1971).

The 1.5% to 2% of the benthos in the drift mode is based on the average of all seasons and for the diel (24-hr) period, to prevent overweighting of the estimate due to periodic influxes of strongly drift-prone animals. Probably 75% of the growth, activity, and production occurs during the 25% of the year when stream temperatures are <20 °C, i.e., June, July, and August in temperate northern latitudes. During winter, and at temperatures of approximately 0 - 10 °C, very little net production occurs. Winter drift rates should be minimal, especially those related to production and behavior. Warm-water summer rates should be high when production is high and animals active. Warm-water drift rates may be several times larger than the typical annual average.

In small steep-gradient streams and those with primarily continuous riffle, there is usually a relative shortage of fish consumers, and the fate of the surplus benthic production is less certain than in streams with large quantities of pool habitat. Considerable quantities may be recycled in these rivers, resulting in loss of production that could be used by fish if the habitat supported larger stocks. In streams with alternating riffle and pool habitat, food production is emphasized in the riffle, and food consumption occurs in the pools. Waters (1962) found this to occur in Valley Creek, Minnesota, with about 66% riffles and 33% pools. This agrees with the long-standing rule-of-thumb that states that the best fish streams usually have half pool and half riffle morphology.

In low-gradient streams, where riffles are nearly absent, we know very little about the drift fauna. In these streams, production can be high because extensive areas of the stream can be occupied by aquatic vegetation or soil areas that support large quantities of benthos, and the fish easily expand into these areas. Also present may be several species of small forage fish, all of which are adapted to the slower velocity rates. Drift undoubtedly occurs in these streams, but data are lacking as to its quantity and fate. It is only speculative, but the drift span is probably a very short distance because of lower velocities. There is probably rapid interception of drift by the majority of fish living in the immediate vicinity of the benthos. Production-induced drift and consumption occur together without separation by time or space sufficient to measure and study the drift in the usual or conventional ways.

FLOW

Velocity is the speed of water or distance traveled in time. Flow is the quantity of water passing a point in unit time. These units are frequently interchanged or confused in communication, e.g., a high or low flow in a reach of stream. Discharge is a flow measurement and is the quantity of water leaving a portion of or the whole drainage basin within a unit of time. Discharge is expressed as cubic feet or meters per second, million gallons per day, acre feet per year, etc. Flow or discharge has volume as well as time. Velocity is a single dimension or distance traveled in time. Thus, flow and discharge are synonymous, but velocity is not.

Flow, Q, is the product of the stream's mean width (w), depth (d), and velocity (v), i.e., $Q = wdv$. A change in velocity will change the discharge, but velocity will change only with a change in depth, because velocity is a result of the surface elevation, or energy, between two longitudinal points along a stream. To increase the elevation or potential energy of the flowing water through a reach, the depth of the river must be increased, because the slope of the bed is fixed. Increasing the depth also effects a change in width (w). The width change is a function of the shape of the channel. Width, depth, and velocity are dependent variables all three change as the volume of water varies (Leopold 1962; Keup 1985).

PRODUCTION OF SUBSTRATE

In a typical reach of flowing water we can expect to find more species of fish food organisms than in an equivalent area of lake, because of the addition of rheophilic animals to the benthic community. In the lake, the substrate may be a relatively uniform plane of material covering an extensive area. This uniform substrate may be highly productive of the few species living there. In the river, a current-swept rock may protrude from a base of fine materials, and one can find rheophilic animals living within inches of soil-burrowing forms. The number of species may be numerous because of the diversity of stream niches, but each kind is limited in numbers by the portion of all habitat that it can occupy. The total biomass of benthos in lakes and streams may be comparable on an areal basis, but in a lake the resources are divided between relatively few species, whereas a stream has many species, each best adapted to its niche among the diverse habitats available.

In a stream, there may be riffles with shallow, swift water separated by pools of deep, slow water. The currents maintain a substrate of various sized particles of material within the riffle by transporting fines downstream, which settle in the slower waters of the pools to blanket the bottom with relatively uniform materials. The benthos within the pool bottom will be less diverse, because of the uniformity of the bottom, when compared to riffle areas.

A stream moving across a plane of alluvium consisting of random assorted particles from colloidal to boulder size would tend to sort the material depending on the velocity of the water at various points within the stream. Currents would suspend the colloids and silts first. The smaller the particle the more resistant it is to resettling and the greater the likelihood to be transported from the watershed or basin. Where velocities are particularly swift and possess the force to move relatively large materials only resistant gravel, cobble and boulders may persist and a shallow rapids or riffle exists. This bottom is resistant to erosion or degradation of the stream bed elevation. An assortment of large materials may overlie a bed of mixed materials that the water has not eroded or cut its channel into. The river created a layer of erosion resistant material that serves as armour overlying mixed basal material.

The channel could be eroded into bedrock, obviously very resistant to degradation of the channel elevation. The bedrock channel will contain assorted materials that are carried into the main stream, via tributaries eroding alluvium and soils from the uplands of the river basin.

Interstitial spaces beneath and between coarse rubble and cobble material are filled with materials of smaller diameter. This smaller material is not affected by the overflowing currents of water because of the protection afforded by the large exposed rocks protruding up from the bottom. This material between the primary substrate is sorted depending upon the amount of protection afforded it. The position of a boulder in relation to the direction and force of the current determines the amount and direction of the currents at different points. The currents will sort and redeposit the embedding materials around the boulder. At different positions around the boulder different size grades of material may be found. Some will be coarse rubble, where stronger currents removed finer material. Finer material settles as soon as the current is reduced and a blanket of sand may cover coarser material in more protected positions around the boulder. The boulder may be flanked by coarse, current-swept rubble and protect a deposition area for fines immediately downstream from the force of the current. The rubble contains interstitial spaces in which stonefly nymphs may live and be afforded refuge from the currents and predators. The sand deposit behind the boulder may be a burrowing site for midge larvae using the sand's protection and incorporated food resources (as the sand was deposited it incorporated particulate organic material within the deposit). The portion of the boulder exposed to the currents is an attachment site for a film of microscopic plant life. Mayfly nymphs capable of coping with currents may graze on this crop of plants. In the swiftest current on the most exposed edge of the boulder caddis larvae anchor themselves with "silk," and spin nets to the current. Moving within their "nest" they wait for the nets to fish particulate food from the current. This boulder has produced at least four microhabitats for four different species and life styles.

Aquatic entomology strongly emphasizes the morphological, behavioral, and other techniques of coping with swift currents by stream benthos. Attempts have been made to determine how swift the currents must be to provide the habitat for rheophilic animals. The problem with these types of investigations is the measurement of velocity within the microhabitat containing the organisms. No measuring device has been made that can measure in microhabitats. Velocity data are usually taken in or near midwater depths. Attempts are then made to relate these data to an organism extending only a millimeter from the bottom into the water column. The theoretical velocity of water at the immediate bottom-water interface is zero, because of the friction between the water and solids. Within a millimeter of the bottom there is velocity, but much less than that measured by the current meter suspended at middepths or even as close to the bottom as possible. To compound the problem, the irregularities of the bottom are on a smaller scale than the current meter, and within these irregularities there is turbulence and highly varied residual velocities. In fact, one may find water flowing upstream in these eddies, as evidenced by the position of some animals that orient themselves to the current. Small changes in flow have been observed to effect the change in position of individual animals upon a single rock as they adjust to seek an optimum available microhabitat resulting from changes in microcurrent force and direction over the rocks surface (Scott 1958; Edington 1965, 1968).

EFFECTS ON ORGANISMS

Scientists have attempted to find animals that indicate the velocity of water in a stream. They have failed for a number of reasons.

1. The organisms are not velocity specific. They exhibit a range, usually quite wide, of preferred velocities. A species with narrow tolerance would have difficulty in surviving.

2. Substrate plays as important a role in microhabitat selection as does velocity. Velocity produces the nature of the substrate, but usually at some time in the past. Flood flows generated the velocities to remove smaller material from the boulder reaches of a riffle. Low flows (drought) would be instrumental in the establishment of beds of fines, e.g., pool bottoms. Though there is movement and sorting at all times at some place within the stream, it is the extreme flows that create the physical habitats. These flows are probably detrimental to the benthos either when substrate is being moved at flood or when it is blanketed by accumulating sediments during drought. Though extreme flows are detrimental to benthic inhabitants, they generate the necessary substrate for the species during the relative continuity of moderate flows.

3. Depth is also a requirement for the benthos. It is not a direct requirement, since many organisms could live in waters barely covering them. Certain depths are required to support the velocities and the substrates essential to the animals. The effective substrate size certainly cannot exceed the depth of the water. The tops of meter-size boulders would emerge from water with a mean depth of

10 cm. With water depths less than the height of the boulder the effective substrate would be the material in which the boulder is embedded, regardless of the coarser material in the "channel." The presence of emergent substrate results in a series of microchannels within the stream. To generate high velocities, depth is required to reduce the turbulence and friction with the bottom. It takes large streams to produce depths (and widths) that will support the highest mean water column velocities. Though mountain streams appear fast, because of the turbulent flows over coarse substrates, the fastest velocities will be found in the flat-water laminar flows of the free-flowing Missouri and Mississippi Rivers. In a stream averaging a half-foot deep, the average cross-section velocity should be about 1.5 ft/s (Keup 1985).

4. It is best to use physical methods to measure physical constituents. Since species must have a range of tolerances to cope with environmental variances, they can tolerate a range of physical limits. The presence of a benthic organism as an indication of a specific velocity would have no apparent value. Figure 8 indicates the estimated maximum and minimum preferred and tolerable velocity ranges for selected rheophilic benthos. The extremes of the tolerable ranges cover an order of magnitude. Figure 8 is based on midwater column velocities, and the range may be considerably less at the substrate-water interface. A range of midwater preferred velocities covering an order of magnitude has limited value, because it exceeds the range of mean velocities one might expect from the smallest (1.0 ft/s) to the largest (5.9 ft/s) rivers in the United States (Keup 1985). One could expect to find these ranges within a stream if the maximum discharges as well as different points within the stream are considered; but the likelihood of the range occurring at a specific point, based solely on discharge, is remote. The absence of a species is probably more indicative of a lack of velocity than is the species presence indicative of a particular velocity. Most species in Figure 8 prefer velocities greater than 0.3 ft/s (10 cm/s). A couple will tolerate velocities less than this, but the length of time is not known.

In summary, we find that there are at least three physical variables that affect the distribution of the rheophilic benthos. Velocity and depth are closely related because certain depths must be maintained to support velocities. The substrate is regulated by the extremes of discharge occurring within the stream during its recent past.

INVERTEBRATE REQUIREMENTS

Gore and Judy (1981) used data from several western United States streams to determine the habitat requirement characteristics of depth, velocity, and substrate for several species of rheophilic benthic invertebrates. Many studies prior to this were related to only one of the physical characteristics, and the use of the data was quite limited. For example, absence or presence of a species could not be related solely to velocity, because

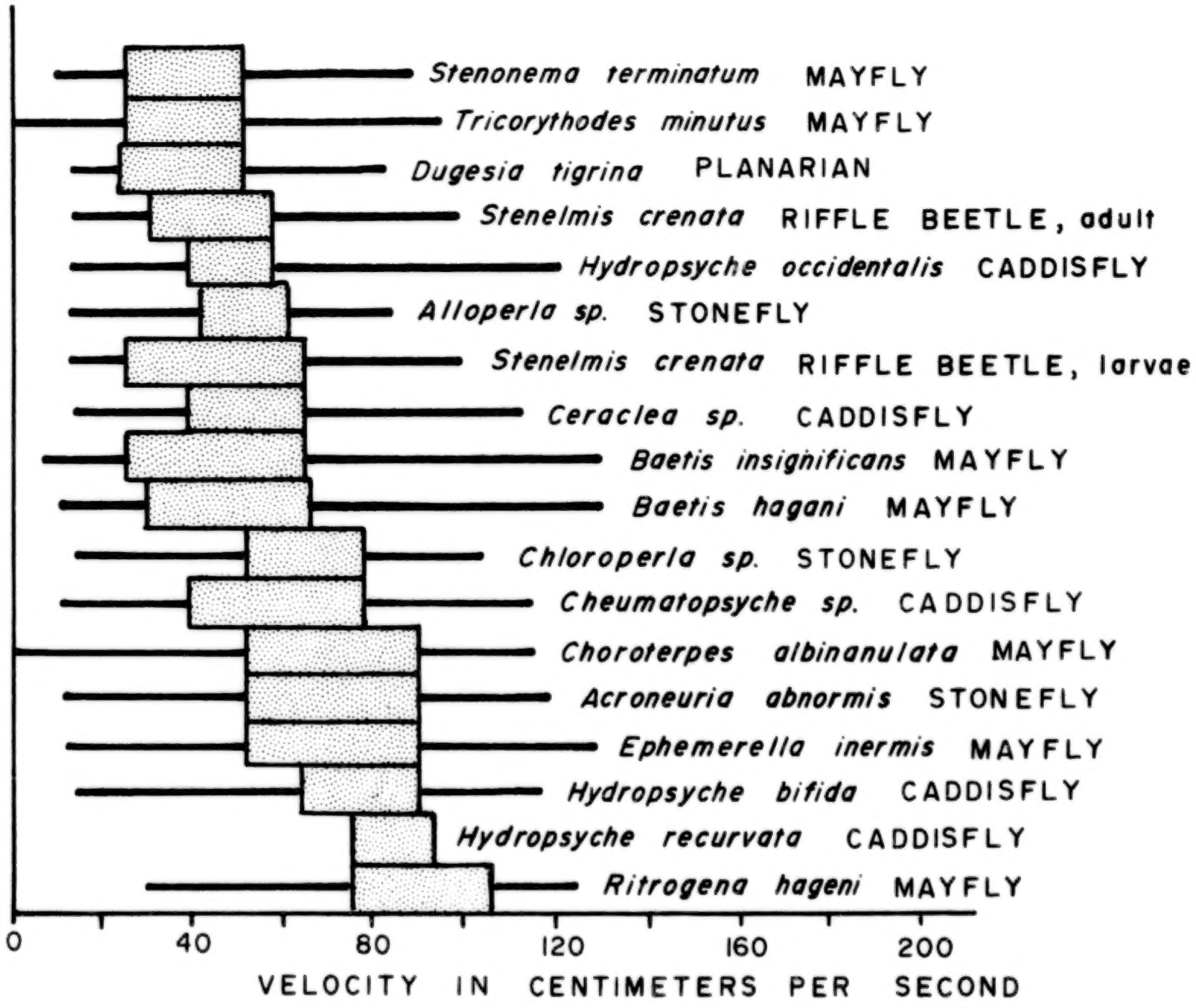

Figure 8. The tolerable and preferred (stippled blocks) velocity ranges for selected aquatic invertebrates (based on data from Gore and Judy 1981).

substrate also affects an animal's presence. At velocity "X," a caddisfly species may be present if cobble is present for attachment, but it would be absent on sand. Attempts to attach to sand may be made by the animal, but the small particle size cannot act as an anchor and the larva is swept away as drift.

Gore and Judy (1981) determined preferred and tolerable conditions of depth, substrate, and velocity. The preferred range reflects where 85% or more of the animals were found, and the tolerable range is an estimate of the extreme conditions in which the animals might occur. Figure 9 summarizes the preferred set of depth, velocity, and substrate conditions for rheophilic species of stoneflies (Plecoptera), caddisflies (Trichoptera), and mayflies (Ephemeroptera). Each species has a preferred pattern of physical habitat needs, but none is unique in its set of conditions. In fact, when the common

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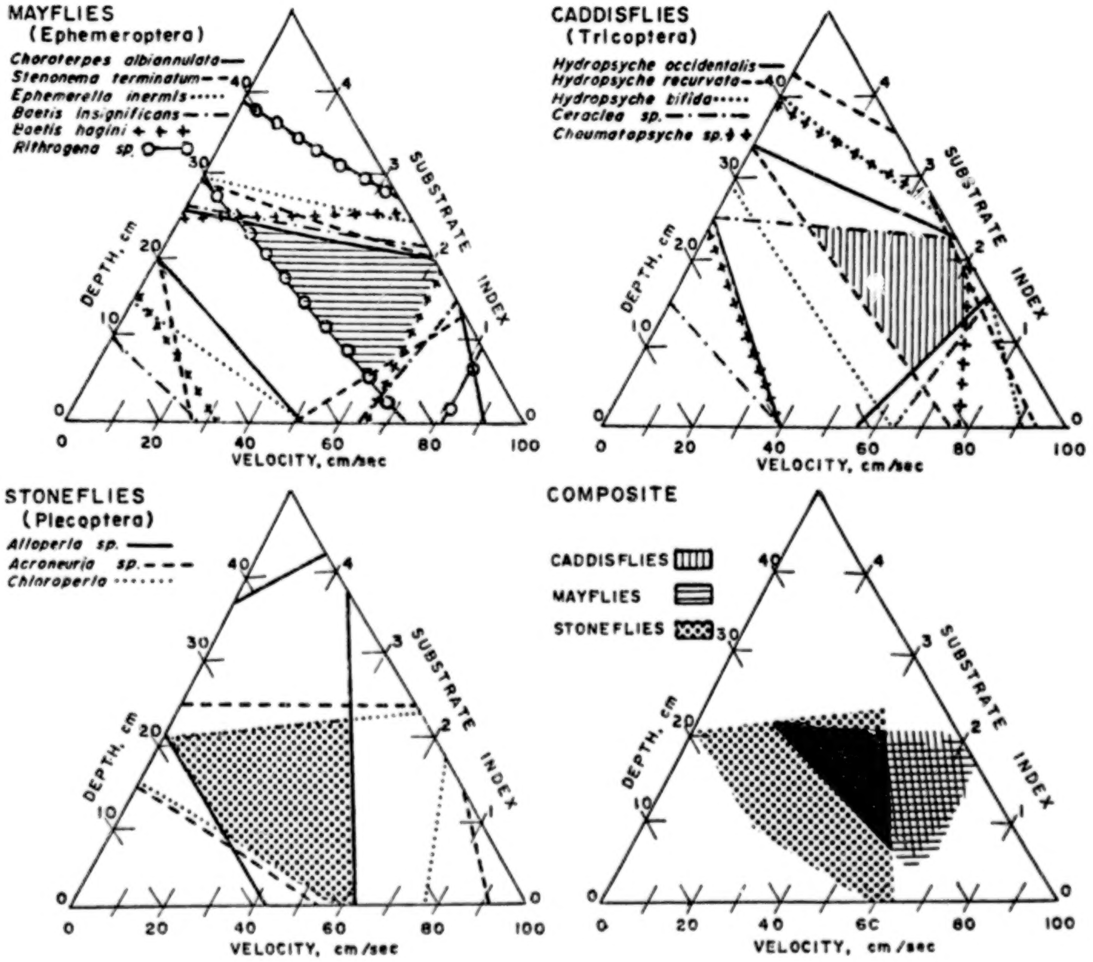

Figure 9. The preferred ranges for the characteristics of depth, velocity, and substrate for 14 mayfly, caddisfly, and stonefly species. The stippled and hatched areas cover the common preferred ranges of the three habitat components for all the species graphed. The composite presentation is the three ordinal hatched and stippled areas. The black area then represents the common preferred habitat for all species plotted (based on data from Gore and Judy 1981).

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preferred physical habitats of the representatives of the three insect orders are overlaid, there is a small set of conditions that is within the preferred range of all 13 species. All 13 species are in preferred habitat having the following physical conditions:

Velocity = 1.8-2.0 ft/s
Depth = 4.3-7.5 inches
Substrate = a mixture of small and medium cobble

These conditions are descriptive of a typical riffle, long considered the important factor for the production of fish food in a stream.

The common preferred habitat described in the previous paragraph would be the "common ground" where all 13 species should be in direct competition. This does not mean that they all would be equally abundant in this habitat. Many other factors besides the physical habitat regulate or influence the well-being of the individuals of a species. The simple fact of competition between 13 species would affect the well-being of the species' populations. An animal species may actually flourish better without competition and where the resources are not partitioned between as many species. For example, in Figure 9, the mayfly (Baetis insignificans) has a preferred depth between about 10 and 15 cm; this is shallower than the preferred range of any of the other species. At depths greater than this, its preferred range begins to overlap with the other mayfly species, including its close relative Baetis hagini. It is quite possible that a species may be most abundant outside its preferred range, but within its tolerable range. Figure 8 shows that two of the species can tolerate velocities of less than 10 cm/s (0.3 ft/s). The lack of space competition, availability of food, and reduced predation may mean these animals are more abundant here. One must remember, however, that some of the less rheophilic species will be competing for space in this velocity.

The species analyzed by Gore and Judy (1981) were from samples from a number of rivers, and it is very likely that species evaluated were not present or common in all the rivers. The invertebrate fauna of riffles is not limited to the species evaluated. In a riffle, one should have no problem finding at least 40 different kinds of aquatic macroinvertebrates, a number about three times the number of species evaluated by Gore and Judy. They evaluated no dipteran larvae, which is the largest order of aquatic insects and includes the many species of midge larvae (Chironomidae, Ceratopogonidae, Dixidae, etc.), or the black fly larvae (Simuliidae), which, with suckers, can inhabit velocities that could not be tolerated by other macroinvertebrates.

Many biologists have been looking for species that are indicators of certain flow regimens. Flow in itself is a product of three variables: width, depth, and velocity. In Figure 8 we see that the velocity tolerance of the species covers ranges near to or in excess of a range in magnitude. Velocity changes of this order within a point in a transact across the river would produce more change in flow than would be found in a century of droughts and floods. The quest for an indicator species that relates to velocity or flow is a futile effort. The animals are too tolerant of velocity variations (Figure 8). A mechanical meter is a much better device to measure velocity.

The addition of more species to Gore and Judy's (1981) analysis would undoubtedly reduce the size of the "common ground" (Figure 9), or eliminate it entirely. It is quite likely, though, that if more species were added to the analysis, the majority would still fall within the same general habitat or use the common habitat illustrated (Figure 9) as an epicenter of physical habitat needs. There is little likelihood of tolerance range not overlapping this area, even if the preferred habitat (85%) did not coincide with this stream region.

The data of Gore and Judy (1981) do indicate that the set of physical criteria for mutual preferred habitat are useful to establish a range of velocities required to support rheophilic animals. None would be excluded. The absence of a species would be due to biological or chemical criteria not being met, or to the species being outside the geographic distribution. Flows less than those required to produce this physical habitat may not eliminate these species but could be detrimental to their well-being.

FLOW MANIPULATION

In streams with regulated flows, the biologist could manage for the wanted percentage of the stream habitat with the preferred velocity characteristics. For example, 25% of the width of the riffles could be managed to produce habitat for the rheophilic organisms, and the remaining 75% would be habitat for animals that preferred lesser velocities. Using the U.S. Fish and Wildlife Service's PHABSIM system (Bovee 1982), a prescription could be prepared to create flow regimens for the support of these velocities.

It is the biologist's problem to determine what types of physical habitat are needed and the proportion of the total stream habitat that should meet those criteria. The biologist must also consider trade-offs between fish food and fish habitat. For example, he might select a large proportion of the stream for the rheophilic fish food organisms; however, this could seriously affect the amount of optimum fish habitat. The physical habitat criteria for salmonid fishes (Bovee 1978) are different than the preferred habitat epicenter for the rheophilic fish food organisms. Optimizing fish food production to the detriment of their consumers--fish--would only benefit the "bugs."

The biologist must also consider that rheophilic invertebrates are not the only foods consumed by fish. I stated previously that fish are opportunistic feeders. Aquatic vegetation will usually support the production of more fish food animals than mineral substrates. Increasing velocity to create preferred habitat for one set of organisms could be detrimental to other equally valuable fish food organisms and could destroy aquatic vegetation along the flanks of a stream. Vegetation supports 3 to 10 times the biomass of gravel or rubble and is important juvenile fish habitat. The ideal situation is to have as much as possible of both habitats. This would provide as diverse a fauna as possible, which influences the reliability of food supply.

Once the biologist establishes the criteria of optimum fish food habitat, the flows necessary to support that habitat becomes the hydrologist's problem. This involves not only a quantity of water, but also that the water fit into a channel, with its morphology. A change in the flow regimen of the river will induce changes in the channel geometry. The channel may be too large or too small for the new flows, and the river will slowly adjust its channel to fit the new hydrologic regimen. The process of adjustment may require many years to stabilize the new channel for the new flows. The estimation of channel fit that will develop in the future involves predictive hydrologic engineering (Simons et al. 1981). One thing is for certain, without man's help the time involved can be estimated in decades.

If a stream's mean base flow were to be reduced from 500 to 100 cfs, one could probably study the channel of a tributary stream to determine the channel morphology of a 100 cfs stream in the same geology and climate. Both the fish biologist and the hydrologist should ascertain the morphology of a new 100 cfs channel within the old 500 cfs channel. Chances are that the projected morphology would provide poor physical habitat for aquatic life. In some decades, the 100 cfs flow will develop a new channel for this flow rate that may be good physical habitat, but until the new channel is achieved, the habitat and the biota will be constantly adjusting. The physical instability associated with the adjustment will mean that fish management will be difficult, and probably impossible, for several decades. Thus, the diversion of 400 cfs could leave a stream of 100 cfs with very little fishery value, although adequate water remains if it were in an appropriate channel. The cost of diversion includes the unpaid for public loss of a fishery for many years. Mitigation for the loss could be part of the cost of the diversion project. Mitigation might involve a fish hatchery to replace natural reproduction lost through burial of spawning gravels when the smaller stream loses sediment transport capacity in the large channel. Mitigation might mean channel modification through structure installation to reduce the channel size and maintain velocities for sediment transport. The latter may be a larger capital cost than the fish hatchery, but it may offset decades of operation and maintenance of the hatchery. Engineering and construction to produce a new channel configuration within a few years may be good management, since it could have benefits beyond the fishery. Riparian habitat could develop on the new stream's banks. A deeper stream will retain cooler temperatures with reduced evaporation. Aesthetics would be enhanced compared to a broad shallow stream meandering within the bottom of a large oversized residual channel.

Once a new flow configuration is prescribed for a stream (based on optimum fish food and fish production), a method must be developed to maintain this habitat. The physical nature of a stream's substrate is not developed or maintained with steady base flows. The periodic (1½ to 2 years) high- or flood-flow interval is a paramount factor in the maintenance of the physical habitat for both benthos and fish (Milhous 1982). Still higher floods occur at less frequent intervals (e.g., 10 and 100 years). These long-interval floods play a role in habitat maintenance, but they also function on a much larger scale, effecting meander frequency, sinuosity, and channel realignment.

The sediment load of a stream (including the bed load) is a factor in stream habitat condition that is closely tied to the water's velocity.

Velocity dictates the available energy to support the transport of suspended materials and the movement of bed materials (bed load). When stream level is falling, velocities are diminishing, the material transport capacity of the water is reduced, and settled materials begin to aggrade the bottom, forming a new benthic habitat of finer materials. With a rising stream level, velocities are increasing, and previously settled material is resuspended or relocated as bed load, thus clearing or restoring the coarser substrates. In a steady-state flow condition, fines will gradually accumulate in the interstices of coarse bottom substrate. For example, sand will travel as bed load and quite rapidly clog gravel or rubble substrate within riffles. This drastically reduces water circulation, which is a requirement for incubating spawn occupying gravel redds. It also degrades the habitat for benthic fish food animals, since only a few species can occupy the interstices of sand compared to the cavities within gravel or cobble. Periodically, flows large enough to generate velocities with sufficient energy to create instability and slight movement in the coarsest substrates must occur. Slight movement of the coarse material eliminates the protection afforded to the accumulated fines, and, almost immediately, the habitat is flushed and the fines are transported out of the riffle reach. A hydraulic engineer with channel morphology and stream transport experience can estimate the flows required for flushing. As a rule-of-thumb, the high flows that occur at about biannual frequencies perform this function.

Periodic disruption of habitat by flood flows is detrimental to the benthos. A portion of the animals is undoubtedly destroyed as the substrate shifts. Many, though, are simply dislodged in a catastrophic drift episode. They return to the bottom where velocities are reduced and persist until the flood recedes. They may migrate back to preferred sites. If a spring flood destroyed half the benthos, the loss would be restored within a month by the growth of the remaining animals. A biannual loss of a substantial portion of the benthos may appear drastic, but it has been occurring for eons, and rapid regrowth of the remaining animals is one of Nature's ways of compensating for the loss. Without periodic flushing, total degradation of the benthic habitat would occur and would be a much more drastic and extended reduction in fish food and fish.

In regulated streams, periodic flushing would be good habitat management. Most regulated streams, however, do not have flush flows incorporated into their flow regimens; flushing only occurs at infrequent intervals when there is more water than the system can cope with. Flush management is analogous to the game managers controlled burn or partial clear-cutting of a mature forest to reestablish the food necessary to maintain deer herds that do not flourish in climax timber. The climax river is bottomed with fines and supports different fish foods and fish fauna than the upstream tributaries. Many of our preferred food and game fish require subclimax streams. Failure to maintain their habitat will result in the invasion of the waters by less desirable species, which then become predominant, regardless of the application of other fish management tools. Without physical stream habitat maintenance and restoration, other efforts in the areas of biological and chemical quality of the habitat can be futile and wasteful.

A major problem is the inability of biologists to prescribe a new flow regimen to maintain a suitable physical habitat when the existing flow regimen is altered. The biologist should prescribe the physical habitat needed for the fish and their food. The flow regimen to develop and maintain physical habitats is within the province of hydraulic engineers. The engineer's skills should not stop at altering flow regimens; it is their responsibility to assist in the best use of the conditions they establish or leave behind.

The achievement of a best future for a waterway subject to human modifications requires the input of all parties involved to achieve the best habitat under the new environmental conditions. The party that fails to participate fails to protect the resource they are responsible for. This includes the developer-manager who must have the economic resources to ensure best residual aquatic habitat, otherwise he is, in the case of fisheries, usurping public resources at no cost. No cost public fishing resources may be the only way a water project can be profitable. The quality of a fishery is not a function of water quantity as much as it is of habitat within the quantity. A little water spread in a large habitat may not be enough at any one point. Conversely, excess water in a small habitat does not enhance it. The solution is to fit water to habitat or adjust the habitat to the quantity of water.

The subject of flows has been of long concern and continues to generate extensive but weakly founded debates. Much debate has been based on the emotions generated when flow patterns are altered by water development projects. These emotions are probably justified, based on the experience of seeing the waters involved "go to hell" as a result of either not enough or excess water dumped into physical habitats completely unrelated to the new streams aquatic life needs. Aquatic life evolved through eons to accommodate physical habitat generated through eons by the natural forces of fluvial hydraulics. Nature has not developed fish or other aquatic life to fit man's production of too much or too little water in a channel during the past century of water manipulation in the United States. A 1,000-cfs channel to carry a 1,000-cfs flow took millennia to develop, and 100-cfs does not fit. The opposite is also true.

The fit of flow to channel is the product of water flowing against earth in variable quantities. This is a product of physics that has existed since creation of the universe. During the Cretaceous, fish evolved with a genetic code to occupy the physics ruled stream habitat. Time has not been sufficient to see genetic shifts in fish to fit a set of artificial physics. Maybe the last major successful genetic change in fish was an accident resulting in frogs and other amphibians that still return to water for egg incubation. The invertebrate fish food is even a more long established stream resident than fish. In an artificial channel, the hydraulic engineer cannot push physics beyond its bounds, or he will not be able to contain or retain the water, even with concrete. He must operate within prescribed limits. The fish manager must also manage within the limits of the habitat requirements of the fish stocks he has to deal with. He does not have a freshwater flounder to dwell in the shoals of a dewatered river channel.

It is only within the past decade that serious effort has started to define a stream's physical habitat and associated biota. This decade-old effort is based on empirical associations of fish and physical habitat. The empirical data currently used may some day allow the discovery of facts upon which to base theory. The biologist need not be hesitant about using empirical information. The professions and expertise he will be working with are also using an empirical base.

The biologist must ask: What will be left after a water development project? A dam and impoundment will trap sediments and release clearer water (maybe more plankton but less mud). The stilling pool below the dam should be deep clear cool water. Trout water? The clear and the cool but not the deep. Recent investigations below Glen Canyon Dam on the Colorado River show that trout do not prefer deep stream waters, especially the young or the trout of the future (Gosse, n.d.). In the Tennessee River valley, deep stilling pools are occupied by catfishes and allied species. Light penetration in water is poor, and trout, sight feeders, stay in the photic zone. Catfish relying less on sight could still use the food swept through penstocks and turbines from the reservoir, but managing for catfish in lieu of trout in western America would be unpalatable.

INSTREAM MAINTENANCE

Sediment removal by a dam could aid in maintaining fish food habitat in downstream reaches for some distance. Less mineral solids (turbidity) would be present in the river. Mineral turbidity, however, could be readily offset by organic materials discharged from the impoundment or grown within the stream. These will accumulate as readily in the interstitial spaces of the substrate as would mineral fines. In addition to the space clogging effect, decomposing organic material can depress dissolved oxygen concentrations, resulting in death for benthos and spawn.

If a dam so regulates flows that flushing does not occur, problems will generally occur within about 10 to 12 miles when a tributary approximately the size of the impounded stream enters. [This is based on the normal distribution of river patterns (Leopold 1962; Keup 1985.)] The tributary will be carrying a sediment load that is discharged to an oversized channel, since the dam is controlling flow, especially peak flow. The channel below the confluence will be that of a stream as much as three times bigger or a stream order larger in size. Sediment transport capacity will be reduced in the large channel, and the food habitat as well as the fish habitat will gradually degrade because of the accumulated sediments. This can be rectified if the dam's operating license requires the discharge of a flow to periodically flush the channel. A multiple-use flood control dam is built to relieve the valley of floods, and the dam's management will argue for no flood, even the flushing flow. This flow is not the property damaging type that the dam was designed to contain. The persons responsible for the fishery should persist. The flush will not create a flood into the flood plain. The management potential for fisheries with a dam is probably as great or greater with the dam than without it, but only if the downstream fishery is part of the water release plan. Each time, the flow regimens are altered to support a new use, the cost of this use includes further fish habitat mitigation to maintain the physical habitat in the altered waters.

Water managers have always had to consider the biological and chemical (water quality) integrity of the fish habitat. Only recently has scientific effort been put forth to incorporate the physical habitat into fisheries management of waterways (Bovee 1982). Physical habitat evaluation and maintenance is a developing science for fish managers. It is not 100% accurate, but its accuracy is rapidly improving as the knowledge base of fish habitat requirements is increased. Its accuracy in prediction is dependent on the hydraulic stream engineer, who is a new breed of scientist on the scene. Both fisheries and stream scientists are learning as they practice their skills, which are not exact but as good as the skills of the other professionals working in water development. The biologist must participate on the team developing water to ensure a good fit of fish, fish food, water, and physical habitat if he desires to have reasonable waters to manage in the future.

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APPENDIX A

TREE SURFACE AREA DETERMINATION

Fallen trees provide cover for fish and substrate for the growth, colonization, and production of periphyton (epidendritic or epixylonic growths, sensu stricto) or aufwuchs [see Weber (1973) for discussion of synonyms]. They are also habitat for macroinvertebrate fish food organisms, they provide shelter and cover for fish.

A living tree toppled into a waterway has a very large surface area for aquatic organism colonization, if we consider all the foliage, twigs, limbs, and trunk or bole. The foliage will persist for a considerable period of time before it is eroded from the twigs. In time, the twigs will erode away, followed eventually by the branches. The trunk may persist for decades as part of the waterway's ecosystem. Determination of the trunk surface area is a simple geometry problem. Excluding the end surfaces of the log, the "bark" surface would be:

$$S = \frac{D_1 + D_2}{2} \pi L$$

where D = diameters of the ends of the log

L = length of the log

To include the ends of a log the surface would be calculated as for a frustrum of a right cone:

$$S = [\pi R_1^2 + \frac{(2 \pi R_1 + 2 \pi R_2)}{2} L + \pi R_2^2]$$

where S = surface area

R = the radii of the ends of the log

L = length of the log

The problem of estimating the surface area, or amount of habitat for benthos, of a complete tree has not been undertaken by limnologists. Within the past decade foresters, especially those concerned with fire potential, logging slash cleanup, logging debris salvage potential and value, and controlled burning programs, have undertaken the analysis of tree crown morphology and composition. Crown weights and composition can be estimated for typical trees of various species based on the diameter at breast height (dbh) of the tree (Brown et al. 1977). The portions (Figure A-1) of different size classes of branchwood and foliage that compose the crown have been tabulated or grouped.

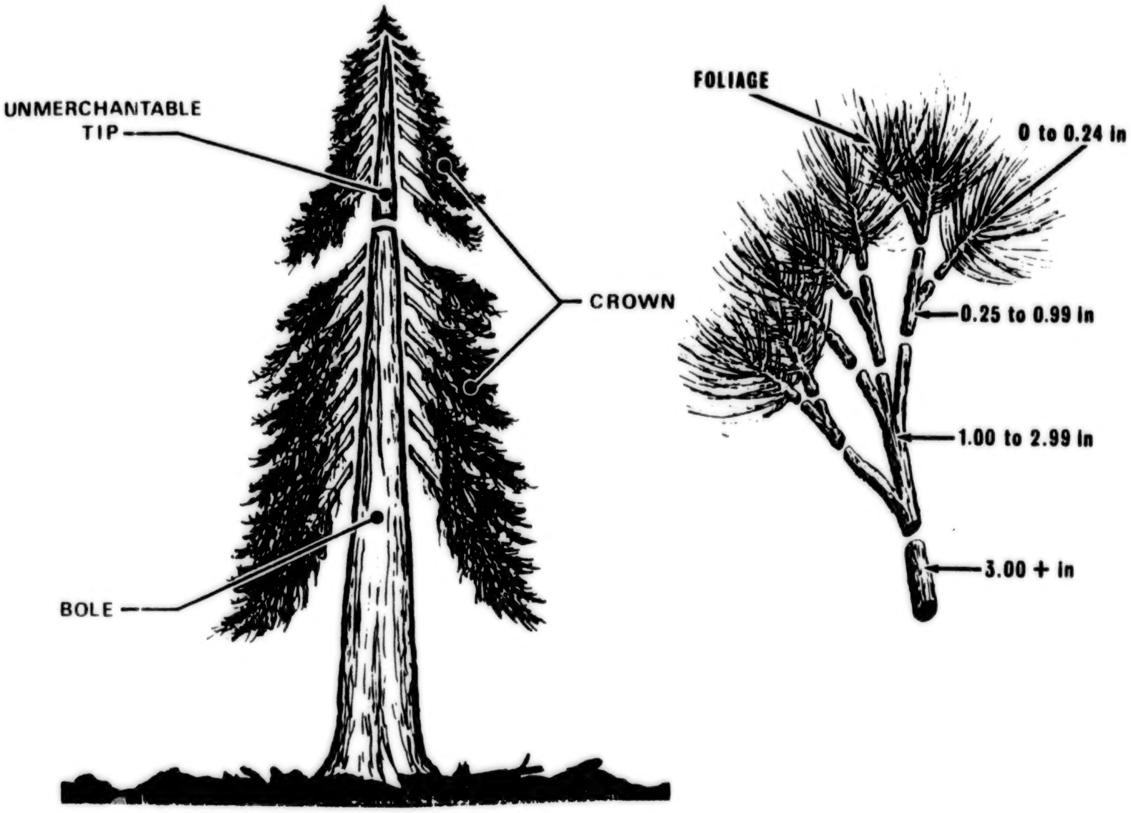

Figure A-1. The components of a tree used in calculating its surface area (redrawn from Brown 1977, 1978).

Total crown weights are known for different size trees by species. The mean diameter of branchwood classes is known. The density or specific gravity is known for different species of wood for many branch size classes. The bole

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extends upward to a diameter of 3 inches* and its surface area can be calculated readily from the formulae presented above.

Table 1 (in the text) presents calculations for the surface area for three species of common Western conifers. The factors or data for making these calculations are as follows:

Branch class: Intervals of branch size classes used by the U.S. Forest Service (see Figure A-1 and Brown 1978).

Fraction of crown weight: From graphs in Brown (1978) or tabular data (Brown et al. 1977).

Crown Weight: From crown weight tables in Brown et al. (1977).

Pounds per cubic foot: Calculated from wood density values (Brown et al. 1977) or specific gravities of diameter size classes (Brown 1974).

Specific gravities for foliage material: Assumed to be 0.5 pound per cubic foot of solids (Brown 1982).

Volume: Calculated from fraction crown weight and pounds per cubic foot volume:

$$\frac{\text{fraction crown weight pounds}}{\text{pounds per cubic foot wood}} = \text{cubic feet}$$

Mean branch diameter (d): Mean values for branch class from Brown (1974).

(Note: Brown's values are for diameter squared, thus the square root of his published values must be used).

s = surface area to volume ratio, or

$$\frac{4}{d} = \frac{2\ \text{radius}}{\text{radius}^2} = \frac{\text{surface area}}{\text{volume area}} = \frac{\text{perimeter length or circumference}}{\text{cross-section area}}$$

Calculated from mean branch diameter for foliage from data presented by Brown (1970).

Metric $\text{cm}^2/\text{cm}^3 \times 30.48$ = English ft^2/ft^3

Surface area (square feet) Volume in cubic feet x s.

---

*If tree tops and slash are encountered where the trunk tip is larger than 3 inches, this larger waste tip or bole fraction must be considered separately, and added to crown totals. It can be done either with geometry using the length of the bole from base to 3 inch diameter and cut-tip diameter. Brown et al. (1977) provide weights of tip boles of 3 inches, 4 inches, and 6 inches. Surface area could be estimated as is done for branchwood using the specific gravity or wood density for the geometric equations presented above.

Bole surface area is based on approximate length of a bole from dbh to the tip (3 inches) for the species at size of dbh indicated (12 inches).

$$\frac{d^1 + d^2}{2} \text{ x length = bole surface area}$$

The data in Table 2 (in text) are for the entire living tree and its fractions. This is the situation occurring if a stream eroded the bank and a tree toppled in. Man or storm-felled riparian trees from beyond the water's edge would need to have compensation made for portions remaining on the stream bank. The critical portion of the estimates is to determine the dbh for the tree, because this measurement is the basis of crown quantity, morphology, and the segment composition.

An aged fallen tree will have fractions of the crown missing. First to disappear would be foliage, then the next class of twigs (Table 2), followed by the next largest, etc. The limnologist would need to classify the condition of the remaining tree by the size class of branches remaining. He could then calculate on the classes remaining, e.g., 3 + 4 + 5 + 6, to obtain surface area remaining. The classes missing would be the portions eroded into the stream and what the trees had contributed in the past to the stream's detrital load or detritus economy for food studies.

A fresh tree toppled into a stream will tend to be one-half submerged. The force of the fall partially collapses the crown structure on the underside of the tree. Most of the weight of the tree is in the bole. If we consider the whole tree at a specific gravity of 0.5, one half of the tree would tend to be submerged before it displaced enough water (buoyancy) to equal the total weight of the tree. The tree will tend to settle to trunk level even if the water is not as deep as half the crown diameter because of: (1) the collapse of the underside of the crown by the tree weight and fracturing of the limbs, and (2) changing stream flows and shifting bed sediments, which cause the tree branches to settle into the bed. After considerable passage of time, the tree will soak water to displace air in the wood. When the remains are water-logged the specific gravity will exceed 1.0, and the tree will sink to the stream bed.

A fresh fallen tree will have approximately half its surface area submerged. Colonization by aquatic organisms will begin immediately. Small surfaces, such as needles and fine twigs, may be too small for many invertebrates to inhabit, but they are adequate and good sites for microorganisms. Grazing fish food organisms will crop the growth. If the growths are not accessible, they will eventually erode away to serve as food for downstream detrital and filter or net-feeding invertebrates. The larger wood also serves as attachment sites for many life styles of fish food organisms, and predatory forms wander through the colony. Fish find shelter and cover within the tree-top maze and reduced current in the crown and behind the bole.

In time, the fine branched wood decays and the pressure of currents, normal and flood, erode the structures away. The eroded material is fractionated into fine particles by the stream. These particles are used by case-building forms and are consumed by detrital feeding animals. Over a period of many years, the tree's biomass is fractionated and available for recycle downstream by many fish food organisms.

This technique must be considered a minimal estimate of surface area. Convolutions in the bark could increase the effective surface area. The values calculated by class or structure fraction could be changed to an effective area by roughness coefficients. The roughness coefficient would need to consider what is significant to the organisms considered. Algal cells could secret themselves in crevices that would be inaccessible to a prowling stonefly nymph, but easily accessible to a first instar midge larvae. It would be possible to partition the habitat to sum that available for the groups of organisms of concern. Algae may occur in all classes (Table 2) remaining on the tree. Mayfly (Trichoptera) nymphs may require classes 3 and larger. Stonefly (Plecoptera) nymph habitat may be limited to classes 4 and larger.

This method allows calculations of habitat space and various fractions contributed by trees in streams. Missing fractions contributed by trees in streams. Missing fractions of downed trees would provide information on the trees' contribution to the food or energy budget of the stream, especially the detrital economy and recycling in ecosystems.

APPENDIX B

ANNOTATED GUIDANCE TO EVALUATION OF FISH FOOD RESOURCES

This appendix is a dichotomous key to assist in evaluating benthos data as a fish food resource. Conclusions resulting from this guidance are to aid the inexperienced person. Persons who have evaluated fish food stocks may do as well relying on their experience, instincts, and intuition to develop an answer to the questions, though a review of this section may stimulate recall of factors to consider.

Bear in mind the words "average," "typical," and "normal." They imply that there are situations less than and greater than these values. Some rivers will be exceptionally good, others bad. Even if all rivers were managed as aquaculture facilities, variance would remain.

KEY

The underlined upper case letters in this key refer to a corresponding annotation in the NOTE section following the key.

1. Fish growth rates and condition factors are average or better .... NO FOOD PROBLEM-A

   Fish growth rates and condition factors are less than average 2

2. Some species of a mixed fish population have less than average condition factors while others are average or better. The latter are harvested species, the poor quality species are not harvested or are underharvested .... A FISH MANAGEMENT PROBLEM. PROBABLY OVERHARVEST OF PREDATORS AND STUNTING OF PREY FISH SPECIES-B

	All species of fish are below normal in condition factor and/or growth rates	3
3.	Condition factors normal, growth rates less than normal	GENETIC OR HABITAT PROBLEM-C
	Fish both stunted and in poor condition	4
4.	Mean flow of stream greater than 1,500 cubic feet per second (7th order or larger)	NOT AMENABLE TO USUAL TECHNOLOGY-D
	Mean flow of stream less than 1,500 cubic feet per second (6th order or smaller)	5
5.	Pool:riffle ratio greater than 2	FOOD PRODUCTION COULD BE LIMITED BY PHYSICAL HABITAT-E
	Pool:riffle ratio less than 2	6
6.	Riffle areas composed of gravels or finer materials	7
	Riffle area primary composition is coarse and large material. Between the primary material there is a diversity of material sizes sorted by currents into a patchwork of particle deposits	8
7.	No coarse material present in river bed or valley alluvium	NATURAL LACK OF RIFFLE PRODUCING MATERIAL. FISH FOOD PRODUCTION MAY BE IN WEED-BEDS, SUBMERGED TREES AND DEBRIS, OR AS BURROWED IN SEDIMENTS-F
	Coarse materials are impacted in fine materials that clogs interstices	SEDIMENT LOAD EXCEEDS STREAM TRANSPORT CAPACITY. USUALLY INDUCED EROSION-G

8.	More than one gram (wet weight) of invertebrate animals per square foot of riffle	9
	Less than one gram (wet weight) of invertebrate animals per square foot of riffle	11
9.	More than 30 kinds of invertebrates found in riffles	FISH FOOD PROBLEM VERY UNLIKELY.
	Less than 30 kinds of invertebrates found in riffles	10
10.	Less than 15 kinds of invertebrate animals found in riffles. A few species may be predominant numerically or in biomass	A NUTRIENT OR ORGANIC POLLUTANT LIKELY PRESENT-H
	Over 15 kinds of invertebrates inhabiting riffles	FISH FOOD PRODUCTION MAY BE SUBOPTIMAL. POLLUTANTS POSSIBLE. FOOD STOCKS MAY LIMIT SELECT FISH SPECIES. PRODUCTION MAY BE LIMITED-I
11.	More than 15 kinds of invertebrates found in riffle areas	FISH FOOD PRODUCTION MAY BE LIMITED-J
	Less than 15 kinds present in riffle areas	FISH FOOD LIMITED. FISH SPECIES DIVERSITY LIKELY LIMITED. TOXIC POLLUTANTS MAY BE PRESENT-K

After manipulating your data through this key you may or may not have found a fish food problem. If you did, you have only identified or diagnosed a problem. Problem solution development, selection of alternatives, obtaining of resources, and implementation remain. If your objective was to know, you are finished; if it was to solve the problem, you are just starting.

NOTES

A

The growth rates may be compared with growth rates found in similar neighboring waters that are known or assumed to be normal. An alternative is to compare the growth rates with those tabulated by Carlander (1969, 1973), selecting those from similar habitats, especially longitude, latitude, and altitude. Judicious selection of comparative data must be made. The most important thing is to compare sites of approximate equal optimum temperatures and growing seasons. Even a coldwater species, such as brook trout, Salvelinus fontinalis, may have a slow growth rate if temperatures are below optimum and growing season is exceptionally short. Under these conditions growth to maturity may take additional years.

Another check for abnormality should be made by using the length-weight relationship (condition factor) to compare populations. Though growth may be slow, the condition of the fish may indicate that their food needs are being met.

If either of the comparisons, growth or condition, indicate the population is within an expected range, the chance of food limitation is remote. Even though an examination of the benthic habitat may indicate a paucity of food stocks, the fish are obtaining sufficient nutrition via another pathway in the food chain. Terrestrial food sources (more likely in small streams than large ones) are important in some waters. The ecosystem may be operating along another line in the food web, such as periphyton or plankton to forage fish to final predator.

B

Forage fish stunting is probably the most common fish management problem resulting from overharvest of predatory species. This situation is exemplified by the farm pond where only bass (Micropterus spp.) are harvested, leaving the bluegill (Lepomis macrochirus) to overpopulate and become stunted. This is less common in open-ended habitats, where there is immigration of predators and emigration of population-pressured forage fish. Stunting may still occur, however, where there is heavy harvest of predator species, such as the bass or pikes (Esox spp.). The best solution is regulation of predator harvest.

In this situation, the fish food expert could be misled if he did not consider the cropping of the fish food stocks. Standing crop of fish food animals may be smaller than expected because of the constant pressure of invertivore fish. The low standing crop numbers can be misleading data to an investigator unaware of the fish stock status and who failed to further evaluate the situation. More food stock information would show very high rates of production for the smaller numbers of invertebrate animals, because competition would be much reduced. A reduction in forage pressure by fish could result in rapid expansion of fish food stock, because of their high reproductive and growth potential.

C

A good condition factor indicates that fish are obtaining adequate food for their length (they are normal or "plump").

A common factor related to slow growth rates is poor habitat conditions. Bluegills, Lepomis macrochirus, are an example of a species that exists, sometimes through introductions, in coldwater habitats that are less than optimum for good growth. Temperatures never reach those needed for good growth; hence the fish are stunted, though other life functions, including reproduction, continue. Coldwater species may also exhibit poor growth rates in abnormally cold water, such as where the water is from glacial or snow pack origins.

D

The streams or rivers that fall into this category are not likely subject to the fish food information or technology presented in the text. These large rivers are naturally much more complex in their ecosystems, since they incorporate faunal and floral components of the lentic as well as the lotic environment. Both the number of scientists and the availability of technology capable of coping with these waters is limited. A problem also exists with the wide dispersal of these systems and zoogeographic isolation or differentiation of the faunas. This affects the ability to transfer information from one system to another. Effects of man's activities on these large rivers has also disrupted the natural continuity of the river. Dredging, dams, navigation structures, and dikes have and continue to interrupt the physical, chemical, and biological aspects of these habitats. A low-head navigation dam can create an extensive lake habitat between typical riverine habitats, neither is the environment of the "wild" river, in which the native flora and fauna evolved. In the pool reach, an investigator would need to use the tools designed for lakes, then switch to riverine tools; however, these were probably designed for smaller habitats. One would not expect the data to readily interface, nor would the technologies used be comparable. In rivers like these, the investigator must rely on his experience and common sense.

E

Based on the ratio of riffles (fish food production areas) to pools (fish production areas), the potential food-growing areas may be in short supply relative to the fish-producing areas. Adequate food stocks may still be available, however (check fish growth rates and condition factors). Overharvesting and poor recruitment could be factors (the standing crop of fish would be below expectations). There could also be excellent supplemental sources of fish food. Food of terrestrial input may be an important supplement; the potential for this increases as the size of the waterway diminishes. Fallen submerged trees and debris collections can be important supplemental habitat for fish food production, as well as fish cover, and should not be overlooked. Check stream for beds of aquatic macrophytes; these can out-produce an equal area of riffles.

F

In valleys of fine alluvial or loess deposits, there simply may not be erosion resistant material present that results in riffle development. In mixed alluvia, e.g., glacial till, a stream will erode the fines away, leaving the coarser material to line the channel. This creates an armored channel that resists cutting. Immediately beneath the armor is a mixture, including fines, that could be eroded if a break were to give the current access. In the meandering of these streams, bed material will be sorted, and bars and riffles of coarse material can be found. These streams may have extensive weed beds containing abundant fish food. The macrophytes appear rooted in fines that only cover the armor, which serves as an anchor for the root structures, making the vegetation tolerant of swift currents. Potamogeton spp., Vallisneria spp., and even the macroalgae Chara spp. and Nitella spp. may effect food production in surplus of fish demand. (Also, see note E immediately above for nonriffle food production sites.)

G

Most commonly a situation that is the result of recent and excessive erosion in the watershed.

Another cause of this problem is the diversion of water, which reduces the stream's transport potential. The channel is oversized for the stream's present flow regime. Water diversion structures can be found. The stream bed is aggrading, and stream bed elevation is increasing. A braided channel pattern can develop. Fish food stocks are relatively poor per unit area of stream bottom. The food production per unit of flow may be equal to prediversion conditions, but the diversity of fish food animals decreases because the habitat becomes uniform with fines distributed in the extensive shoal waters. Though fish food production may exceed presiltation conditions, the production is academic, because the physical habitat needs of the game fish populations are destroyed. The river may support large quantities of minnows, which feed on the surviving species of Diptera larvae and Ephemeroptera nymphs. The few surviving fish species flourish, in part, because of a lack of piscivorous fish species.

These same causes and effects can occur naturally in limited reaches of a natural stream. Streams with glacial sources are subjected to excessive loads of mineral sediments as the glacier melts. Where there is an abrupt decrease in stream gradient, extensive alluvial deposits may occur. Streams, upon leaving mountainous areas and entering a plain, have a loss of gradient or energy, which reduces their ability to transport material. Extensive alluvial deposits, frequently with braided channels, can be found in the transition area between mountain and plain. Being a transition zone, one may expect both mountain and plain aquatic fauna to be present. Neither will prosper because of the relatively poor habitat and the division of resources between a greater variety of species. These foothill areas are essentially confined to some western mountain regions, where there is a great potential for elevation change and rapid decline of gradient. The eastern Appalachian and Alleghany Mountains have a less rapid transition to the plains.

H

Most likely, the reach of river is impacted by the effects of either organic or nutrient pollutant(s). Organic materials, or those grown from the nutrients (periphyton), cover the riffle habitat, eliminating the diversity of niches, which reduces the variety of life. Surviving species do extremely well because the space available to them expands, competition from other species decreases, and there is a great supplement of nutritional material available.

You have not discovered pollution. Unless familiar with this problem obtain help from a water quality biologist. Water pollution assessment with abatement requires:

A - Assessment of damage(s)
B - Determination of cause(s)
C - Control measures.

At this point you have only assessed an atypical fish food crop that may be related to a source of pollutant material(s). The source(s) and the causative agent(s) must be found and quantified and then source responsibilities determined.

I

Highly specialized studies may be needed at this juncture. The impacts may only be marginal. Food limits may impact only select species of fish. Fish food production may remain high and nonconventional techniques, such as drift (Chapter III), may be appropriate considerations.

J

There are likely 30 or more kinds of invertebrates present. The basic production of the stream may be limited and the sparse numbers reduce the variety taken per unit of collection effort. Here a species becomes rare even though its relative contribution to the sparse community does not change. (Annotation "I" may also be appropriate.)

K

Toxic materials eliminate sensitive species. As the concentrations and time of exposure increase more species are eliminated. The number of organisms per species surviving may increase because of reduced interspecific competition. The total biomass of the community will remain about the same or may even increase slightly. The materials may not be toxic to the surviving tolerant species but there are not substantial benefits, such as nutrient or food, to the surviving community's few remaining species. You have not discovered pollution (see annotation "H"). Such conditions do occur in nature where salinity, temperature, or other environmental factors become intolerable for the usual spectrum of species, and only a few flourish.

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Fish are the aquatic ecosystem's end product harvested by man. Food supply may regulate the production of fish. This report deals with analysis and evaluation of fish food stocks. The scope is limited to river habitats and their invertebrate supplies of food. Information is most applicable to smaller streams or rivers--up to mean annual discharges of approximately 1,000 cfs.

Emphasis is placed on the macroinvertebrate (visible to the naked eye) food animals. These are the primary food items of the carnivorous sport and food fishes (e.g., trout, bass, etc.) that are of high management interest.

Three main sections discuss (1) the habitat of fish food animals, (2) the "drift" phenomenon, and (3) the effects of flow on the habitat and organisms.

Aquatic vegetation, logs, or debris in a stream increase the physical habitat available for benthic animals. A method is presented to estimate the area of habitat available from tree remains in a stream.

A "key" is presented to aid managers in a cursory examination of fish and fish food information. The key assists in narrowing the range of potential problems managers need to consider in evaluating a river's biological resources.

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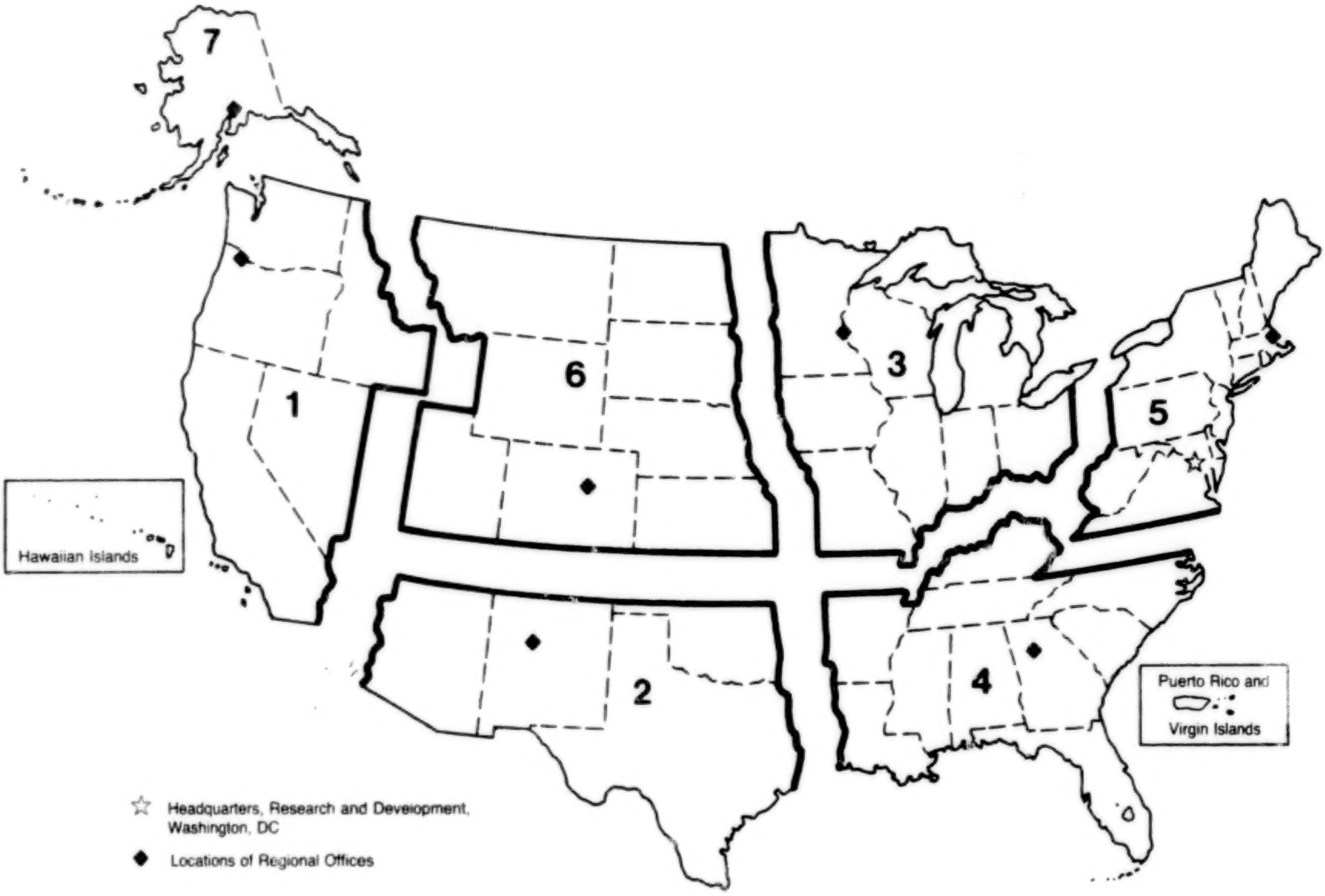
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